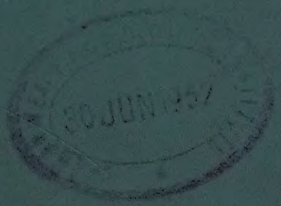
PAPERS OF THE MICHIGAN ACADEMY OF SCIENCE ARTS AND LETTERS

XXXVI (1950)

PART I: BOTANY AND FORESTRY



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PAPERS OF THE MICHIGAN ACADEMY OF SCIENCE ARTS AND LETTERS

EDITORS
EUGENE S. McCARTNEY
FREDERICK K. SPARROW

VOLUME XXXVI (1950)

PART I: BOTANY AND FORESTRY

"Pusilla res mundus est nisi in illo
quod quaerat omnis mundus habeat."
— SENECA, *Naturales Quaestiones*

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BOTANY

SEASONAL ASPECTS OF THE BERMUDA ALGAL FLORA*

ALBERT J. BERNATOWICZ

FLORISTIC studies of the algae of Bermuda have been published by Collins and Hervey (1917) and by Howe (1918). The work of Collins and Hervey is especially useful, since it is based on their own extensive collections over a period of six years and on the smaller collections of earlier authors. Howe made no attempt to report a complete list of species, but he furnished interesting and valuable descriptive remarks on some of the more common species. Although these authors mention that certain species have "their seasons," they give no indication of the extent of the seasonal changes which occur. Field observations by the writer from February to mid-September, 1949, disclosed the seasonal variations of the algal flora to be sufficient to affect the aspects of some areas.

Considerable changes in the algal flora take place notwithstanding the uniform and mild climate. The temperature range covers only about eleven degrees centigrade. Air temperatures in February and March average from 18.5° to 21.5° C.; in May and June they fluctuate from 23.5° to 25.5° C., and August brings the warmest days of the year, with temperatures about 29.5° C. The sea is generally one to three degrees cooler than the air. The mean tide range is about 2.4 feet, and the mean spring range is about 3 feet.

At all seasons in calm areas a short fuzz of several more or less generally distributed species covered the rocks between tide marks. *Bostrychia tenella* (Vahl) J. Ag. and *Polysiphonia Howei* Hollenberg persisted about high-water mark practically everywhere. There were none of the large intertidal forms such as are found on northern shores. Whatever seasonal changes may have taken place above low-tide level did not appreciably alter the aspects of the communities there.

The communities in three types of habitat near and below low-tide level were studied frequently between late winter and early autumn. The first of these habitat types, a landlocked salt-water pool or fishpond, is

*Contribution from the Department of Botany, University of Michigan, No. 924, and from the Bermuda Biological Station for Research, No. 162.

extremely well shaded and protected from wave action. The largest of these pools is only ten feet in diameter and six feet deep at low tide. They are often more nearly six feet in diameter and two feet deep. Steep rock sides surround these pools, but there is always tidal access, either through small openings in the walls or through underground connections with the sea. As a rule, the ponds are heavily shaded by trees or ledges. The bottoms are commonly of soft mud over coquina.

These pools displayed a richer flora during February and March than did any other habitat. *Bryopsis plumosa* (Huds.) C. Ag., *B. hypnoides* Lamx., *Monostroma latissimum* (Kütz.) Wittr., and *Halymenia bermudensis* Collins and Howe were the most conspicuous species. Toward the end of March *Ulva Lactuca* L. also became prominent. *Caulerpa racemosa* (Forssk.) J. Ag., *C. crassifolia* (C. Ag.) J. Ag., and *C. sertularioides* (Gmel.) Howe were present but less obvious. *Caulerpa racemosa* is of particular interest because it was the only species also common in the two other habitats to be described. These few species steadily increased in quantity, so that in April the pool vegetation was luxuriant, with no one species dominant.

The luxuriance was even more pronounced by late spring or early summer, when Bryopsis choked the pools. Ulva and the species of Caulerpa were still important members of the community. Monostroma and Halymenia were fading, and disappeared in June. No new important species were recognized. In contrast, the late summer and early fall vegetation of August and September in the pools was sparse, being dominated by tufts of Myxophyceae. Bryopsis was scanty or lacking, and the blade-like Monostroma, Ulva, and Halymenia species were altogether absent. Although *Caulerpa crassifolia* and *C. sertularioides* were still rather abundant, *C. racemosa* persisted only in the most shaded niches.

The general impressions obtained from small, easily scanned pools are more likely to be accurate than those formed from viewing the next type of habitat to be discussed, which may be called "Thalassia-cove type." Such a sunny, calm cove is typically 150 to 300 feet long and about as wide. The water is usually shallow enough to permit wading, and the bottom is covered with beds of the turtle grass *Thalassia testudinum* Konig and Sims. A mangrove thicket (*Rhizophora Mangle* L.) is commonly found at the head of the cove. The button bush, *Conocarpus erecta* L., and the black mangrove, *Avicennia nitida* Jacq., line the smooth coquina sides. A narrow shelf of rock extends a few feet from the sides of the cove and then drops several inches to a bottom of gritty,

calcareous mud, which smells of hydrogen sulfide. Little wave action disturbs the waters. The mangrove thicket and its dominant algal component, the Bostrychia complex, belong to a distinctive ecosystem, which will not be considered at this time.

The flora of such a cove in February and March was particularly monotonous. The dominant alga was a Sargassum, the leaves of which were covered with silt and detritus. Second in abundance were two of the Rhodophyceae, *Amphiroa fragilissima* (L.) Lamx. and *Spyridia filamentosa* (Wulf.) Harvey. Spyridia, afloat or attached near the shore, was of an unsightly buff color. The Amphiroa had the same bleached color, but grew on the bottom as a cover through which blades of Thalassia protruded. Two species of Phaeophyceae, *Scytosiphon Lomentaria* (Lyngbye) C. Ag. and *Aegira Zosterae* (Mohr) Fries, were prominent in February. Scytosiphon was restricted to areas covered by only a few inches of water at low tide, while the stands of Aegira extended to a depth of three feet or more. The two species soon became scarcer and they were absent in April. The genera Sargassum, Spyridia, Amphiroa, Scytosiphon, and Aegira may be said to be responsible for the drab appearance of these coves in winter and early spring. In addition, a myxophycean scum of *Lyngbya majuscula* Gom. was present in some areas and locally changed the appearance. The Chlorophyceae were represented mainly by a few epiphytized calcareous members of the Codiaceae and by *Cymopolia barbata* (L.) Lamx. *Caulerpa racemosa* existed in small quantity and did not develop as rapidly here as it did in fishponds.

During late spring and the beginning of summer there seemed to have been very little noticeable change. This superficial similarity was due largely to the continuing dominance of the drab Sargassum, Spyridia, and Amphiroa. Scytosiphon and Aegira were lacking, however; the phaeophycean genera were now *Padina* and *Dictyota*. Moreover, the number of Cymopolia and Caulerpa had increased. Clean young green plants of the Codiaceae, including *Halimeda Monile* (Ell. and Sol.) Lamx., *H. tridens* (Ell. and Sol.) Lamx., *Udotea Flabellum* (Ell. and Sol.) Howe, *Penicillus capitatus* Lamk., and *Avrainvillea sp.*, were present in the beds of Thalassia. At this time the scum of Lyngbya was supplemented by increasingly frequent gelatinous tufts of *Symploca hydnoides* Gom. A new red alga, *Acanthophora spicifera* (Vahl) Børg., arose and quickly became conspicuous during this season. During the transition from spring to summer, then, new species of Phaeophyceae began to appear; among the Chlorophyceae the change was more in numbers of thalli than

in species. The Rhodophyceae and the Myxophyceae changed relatively little either in species or in numbers during the same period.

Although the aspects of the earlier seasons were determined mainly by the drabness of Sargassum, Spyridia, and Amphiroa, the late-summer appearance of the quiet coves depended upon an abundance of calcareous forms and Myxophyceae. The most important change in August was probably the disappearance of Spyridia from near the surface, with consequent exposure of the steadily increasing Codiaceae and Dasycladaceae. Of these families, Halimeda, Penicillus, Udotea, Cymopolia, *Neomeris annulata* Dickie, and *Acetabularia crenulata* Lamx. are calcified, and at this season they flourished. In particular, Acetabularia made a field of tiny parasols, which during low tide was barely immersed in some parts of the coves. Among the Phaeophyceae a calcareous species of Padina was as abundant as it had been in June and added to the general impression that the flora was largely of calcareous algae. Coincident with this dominance of calcareous green and brown algae there was a decrease of the calcareous red alga Amphiroa. The general increase among calcareous forms was accompanied by an increase of the two blue-green species, *Lyngbya majuscula* and *Symploca hydnoides*. Growing at the surface of the water, here and there they obscured the bottom dwellers.

In summarizing the seasonal aspects of the calm and sunny Thalassia coves we note that the monotonous colorless flora of winter became more interesting in late spring because of the arrival of two new brown algae and the increase of green calcareous forms. The calcareous forms continued to increase until they dominated the bottom in late summer, when they were locally hidden by blue-green algae of the surface waters.

The third type of habitat consists of surf-swept rocky shores. Although characterized by somewhat more active waters than are the previous areas, the situation is not one of heavy wave action. The shore is of coquina, eroded into a mass of knife edges. It rises abruptly from the water, sometimes in clifflike proportions. The continuous algal fuzz of calmer shores is largely lacking, possibly because of the scouring action of the surf. Occasional small and shallow rock pools dot the shore. The rock bottom is interrupted at frequent intervals by patches of sand and coral heads. The slope of the bottom is steeper than that of mud bottoms; nevertheless, within fifty feet of the shore it is probably no more than ten feet below low-tide level.

A characteristic feature of such shores in February and March was the abundance of small things. There was a wealth of species, but the

plants were poorly developed, and few of the species grew in great quantity. Sargassum, scrubby at low-tide level but larger in deeper water, was dominant. Of the several other Phaeophyceae to be found only *Dictyopteris Justii* Lamx. and *Colpomenia sinuosa* (Roth) Derbes and Solier were conspicuous, although neither was at full size. Several species of Dictyota appeared in March. Among the green algae the ubiquitous *Caulerpa racemosa,* still small, was more frequent here than in either of the previous locales at the same season. *Codium intertextum* Collins and Hervey, a prostrate species, was rare in February but became abundant in March. During March a few rhodophycean species were sufficiently evident to make these shores much more colorful than were the quiet coves. These red algae included *Dasya sp., Laurencia sp., Lophocladia trichoclados* (Mertens) Schmitz, *Dudresnaya crassa* Howe, *Trichogloea Herveyi* Setchell, and several species of Liagora.

Many of the small plants never became large or abundant enough to affect the overall appearance, but some were rapid growers and flourished by late spring. *Caulerpa racemosa,* for example, grew to full size and luxuriance in May. *Codium intertextum* retained its early prominence. Colpomenia reached a magnificent maximum early in May and was fading in June. Indeed, it and the other Phaeophyceae dominated the scene during May and June. Sargassum, Dictyopteris, and *Zonaria zonalis* (Lamx.) Howe did so by virtue of their relatively great size while *Pocockiella variegata* (Lamx.) Papenf. stood out by its great abundance. The red algae, on the other hand, almost disappeared. Of the earlier inhabitants only Lophocladia remained abundant, and a single new arrival, *Laurencia obtusa* (Huds.) Lamx., added a little variety.

In late summer the changes were again very pronounced. *Caulerpa racemosa* and *Codium intertextum,* though still present in quantity, seemed past their maxima in both numbers and vigor. The brown algae were still dominant but were obviously waning. For example, Dictyopteris had reached its largest size, but the plants were battered and epiphytized. Pocockiella, still plentiful, was not so generally distributed as before, which seemed to indicate that some of the colonies had died out. And the great masses of Colpomenia were quite gone. The Rhodophyceae fared worst of all, for not a single species was seen in quantity sufficient to make a mark on the overall aspect. Instead, frequent gelatinous tufts of Myxophyceae floated from the remnants of larger algae and somehow added to the impression of a moribund flora.

We may summarize the aspects of surf-swept rocky shores as charac-

terized in the early spring by numerous small, perhaps young, plants. The red algae for the most part showed only a brief period of abundance; the brown algae grew rapidly and persisted to dominate the summer scene, showing signs of diminishing only in August or September. As in both the calmer habitats, Myxophyceae were important members of the community in late summer. Furthermore, *Caulerpa racemosa* appeared in quantity earlier and persisted later here than in either of the quiet areas. In each situation it was a rock Caulerpa under consideration, but no attempt has been made to compare the several varieties and forms of *Caulerpa racemosa* from each habitat.

A logical extension of these descriptions of habitats and aspects would include the most active waters, that is, the outer reef areas. Unfortunately, these rough waters did not permit enough observations to furnish a report.

The writer wishes to express his thanks to Professor Wm. Randolph Taylor, of the University of Michigan, for his guidance and for the opportunity to undertake these studies as his research assistant. Through the kindness and coöperation of Professor Dugald E. S. Brown, formerly director of the Bermuda Biological Station, the author was provided with the necessary facilities.

University of Michigan

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PERMANENT MOUNTS OF AGAR PLATES OF STREPTOMYCES FOR USE AS HERBARIUM SPECIMENS*

KENNETH LESTER JONES

MANY authors in describing species of Streptomyces have given little or no information on the characteristics of colonies on agar or gelatin plates. Consequently, in the latest edition of *Bergey's Manual*[1] colonies are not even mentioned in the descriptions of thirty-five of the seventy-three recognized species. Organisms as well known as *Streptomyces griseus* and *S. lavendulae* do not have colony descriptions.

I believe that colonies of Streptomyces possess convenient macroscopic characteristics of taxonomic validity that are not duplicated in larger and less definite growths on slopes and plates. These include size, shape, nature of the margin, topography, position of the aerial mycelium, color of the colony and of the surrounding medium, and tendency to produce sectors.

Colonies must be grown in a standard manner to give significant data for analysis and comparisons. This requires: (1) the use of organisms freshly isolated from natural substrata, or at least vigorous organisms of known cultural history; (2) media of known chemical composition; (3) a set plan of inoculation (Pl. I); and (4) constant physical conditions.

Anyone who has cultured only bacterial colonies has a surprise in store for himself when he first grows Streptomyces. Given conditions for full development, some species produce elaborate colonies. For example, I have one species, especially interesting because it is from Bikini, in which the aerial growth takes on a pattern of green, brown, flesh-colored, and white areas against a brilliant orange vegetative base. One has been observed in which the colony is hollow with a central pore, exposing coralloid growths lining the interior. Another develops a leathery stroma which cracks into concentric platelets that are thrust upward on edge.

*Paper from the Department of Botany, University of Michigan, No. 920. Financial aid was given by Horace H. Rackham Faculty Research Grant No. 703.

[1] Bergey, D. H., and Others, *Bergey's Manual of Determinative Bacteriology*, Sixth Edition, xvi + 1529. Baltimore: Williams and Wilkins Co., 1948.

Quantitative characteristics, including the frequency of sectors, may be analyzed statistically when hundreds or thousands of colonies of a given isolate are grown in a standard manner. In such colonies size, for example, is an index of growth rate and of the chemical and physical relationships between colonies. Relatively few isolates, in my experience, have a strong tendency to sector or to exhibit a wide range of fluctuating variations.

Although taxonomic works do not at the present time make it possible to take advantage of the rich criteria that colonies of Streptomyces afford for the identification of species, nonetheless these criteria are useful in other ways, for example, in the preliminary sorting of isolates from a given soil and in comparing those of one soil with another to get some idea of natural distribution.

Fortunately, permanent preparations of the agar plates containing the colonies can readily be made as follows: A 1 : 1,000 dilution of $HgCl_2$ is carefully poured on the agar plates and left there for a half hour. The entire agar plate is then lifted as a thin disk from a petri dish with the aid of a spatula and is placed intact on filter paper. I use a size of paper sufficient to accommodate four agar plates with their labels. A few sheets of filter paper are placed on the agar and the process is repeated until about six layers of specimens are in the pile. A slight weight such as a magazine or two is placed on them, and the material is left to air-dry at room temperature. The filter paper is changed after two days to facilitate drying and to prevent the agar from adhering to the paper. When thoroughly dry, the agar plates are cellophane-like films that retain their colors remarkably well. The films are placed in transparent envelopes and filed in drawers or mounted on standard herbarium sheets (Pl. I).

A few words of caution may be helpful. The original layer of agar medium should be fairly thick, say, 3 mm., and of a 2 per cent agar content. A thinner plating or a more dilute agar will result in the disk breaking or folding when it is lifted from the petri dish. The other extreme is apt to be equally unsatisfactory since the vegetative stroma of a colony may contract at the time of sporulation and crack heavy agar into irregular chunks. If the bath of bichloride is left on the agar too long, the physical composition of the gel is affected, so that the dry films crumble to powder when handled. Treatment with the bichloride kills the Streptomyces, which is a necessary precautionary measure, but it also permanently protects the agar against any possible microbial contamination,

which here would be rapid and ruinous. Fungicides or killing agents containing alcohol darken most of the colonies instantaneously.

Sometimes excellent specimens are obtained when agar disks are directly exposed to the air on a suitable flat surface, without weighting them down with absorbent papers. Unfortunately, the films are apt to curl as they dry, for the margins pull away from the underlying paper. Too heavy a weight on stacks of drying plates flattens the colonies unduly and causes the agar to stick to the paper. The same degree of care must be exercised in handling the dried agar films that is required in working with herbarium specimens of flowering plants, since both are crisp and will crumble if maltreated. A relatively few isolates bear their spores so loosely that they are mostly lost when the bichloride solution is applied or in the subsequent contact with paper. I have not solved this difficulty, but I believe that a film of quick-drying adhesive, applied before flooding the plate, might prove satisfactory.

The dried specimens admittedly do not show the form and structure of the colonies as well as do the fresh cultures because a flattening and shrinking occur. They make it possible, however, to assemble and compare thousands of isolates at one time, which is entirely out of the question with living cultures. It is also important to have permanent records of actual material of organisms freshly isolated from nature, where, as in Streptomyces, variation is a major problem and many isolates do not survive laboratory conditions.

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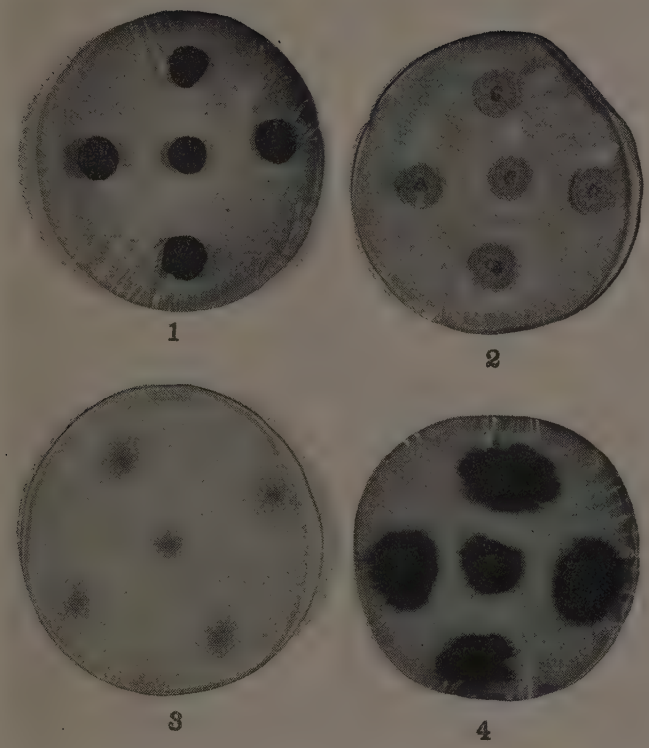
PLATE I



Permanent dried and sterilized agar plates of Streptomyces isolates from soil: (1) Number IV–40 on Bennett's medium; (2) Number I–67 on Czapek's medium; (3) Number I–5 on Czapek's medium; and (4) Number I–18 on Bennett's medium

THE DEVELOPMENT OF THE YOUNG VEGETATIVE MYCELIUM IN STREPTOMYCES*

KENNETH LESTER JONES

NO ONE, so far as I am aware, has given special attention to the development of the young vegetative mycelium of Streptomyces. Several investigators, including Waksman (1919), Drechsler (1919*a–b*), Lieske (1921), Carvajal (1947), and Klieneberger-Nobel (1947) have briefly commented on the subject or presented illustrations. McClung (1949) has studied intensively many species of the allied genus Nocardia (Proactinomyces).

In the present work spores or aerial hyphae of Streptomyces were germinated and studied on glycerol nutrient agar blocks according to the method of Jones (1940) as improved by McClung (1949). After twelve hours of incubation at 22° C. the mounts were first observed microscopically. Most isolated spores and fragments of filaments do not germinate, as McClung (1949) found true of Nocardia filaments. Camera lucida drawings were made under a 4-mm. objective at intervals of one to two hours of growing material, which was kept at 22° C. in moist chambers when not under observation.

The text figures for this paper have been selected from several dozen studies to illustrate the main findings. Generally, spores of Streptomyces germinate at two opposite positions at different times (Figs. 10*a–b*), and hence the germ tubes are unequal (Fig. 1*a*). Short aerial hyphae that occur in the suspensions with the spores may also grow at both ends (Fig. 4), as McClung (1949) illustrated for Nocardia, which is asporous. Usually a primary filament curves near each end, so that the direction of the tips is reversed (Figs. 1*d* and 11*c*), or it produces one or more sharp curves centrally (Figs. 6, 7, and 10).

The curved ends may grow alongside the median portion of the main hypha or its branches (Figs. 2–3). Laterals may change their original course and become parallel to and even press against the primary filament

*Paper from the Department of Botany, University of Michigan, No. 921. Financial aid was given by Horace H. Rackham Faculty Research Grant No. 703.

(Figs. 4*d* and 5) or against one another. They grow toward one another as though mutually attracted by a stimulus and, once aligned, they do not cross but continue to elongate, whether headed in the same or opposite directions. This phenomenon may occur between filaments of separate colonies that happen to be proximate. Fascicles of as many as six strands have been seen in growths older than those illustrated in this paper. This kind of organization, incidentally, is found in the coralloid aerial growths visible macroscopically on some colonies; for an example see Lieske (1921), p. 79. The affinity of hyphae also calls to mind the belief of Klieneberger-Nobel (1947) that there is a fusion of filaments in the primary mycelium to form initial cells "which consist of darkly staining nuclear bodies surrounded by cytoplasm and later enclosed by a cell wall." The initial cells are supposed to produce the diploid aerial mycelium.

The curved median portion of a primary filament serves as a center for the development of hyphae that will radiate outwardly to form very early a symmetrical growth, circular in outline. Such an individual is almost from its inception veritably an "actinomycete" or ray fungus. Figure 10 shows this happening from a sigmoid curved portion, and Figure 7 represents it from a region that is bent into a circle.

Thus, in the material that I have studied, the initial filament usually loses its position of dominance very early (Figures 4 and 5 show exceptions). Lieske's illustrations (1921, pp. 53 and 62) agree. McClung (1949) found that in the closely related species of Nocardia which have persistent mycelia the initial filament commonly remains dominant for a much longer time.

If a spore has only one germ tube (Fig. 9), the primary hypha may become contorted and stunted, but the laterals may be vigorous and overgrow one another and thus form a complex network. Drechsler (1919b) illustrated such germ tubes and also spores with two and three tubes, as did Carvajal (1947) in his interesting photographs of submerged growths.

The present investigation is exploratory. Its findings so far do not offer much encouragement to the taxonomist since the results from a single strain are so variable in some instances (Figs. 4–8). I believe, however, that more organisms must be studied before the characteristics of young vegetative mycelia can be relegated to the long list of invalid ones for this enormous and difficult genus. Drechsler (1919a), who was hopeful of establishing specific characteristics, stated: "From 1 to 4 germ tubes are then produced, apparently more or less successfully, the ap-

proximate number being, in a measure, characteristic of the species. Specific characteristics are expressed also in the diameter of the hyphae, and in the frequency of branching." McClung (1949) did not find specific differences between species of Nocardia that form an extensive mycelia and are most like Streptomyces. Whatever its taxonomic implications, I believe that developmental studies of the young vegetative mycelium will elucidate our ideas on growth, morphogenesis, and nutrition in a genus of considerable practical importance to man.

University of Michigan

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NOTE

All the drawings were made with the aid of a camera lucida by means of a 4-mm. objective and a 12.5 ocular, and all are to the same scale. The bar scale on each figure represents ten microns. The material grew on glycerol nutrient agar blocks and was kept at about 22° C., except as otherwise stated.

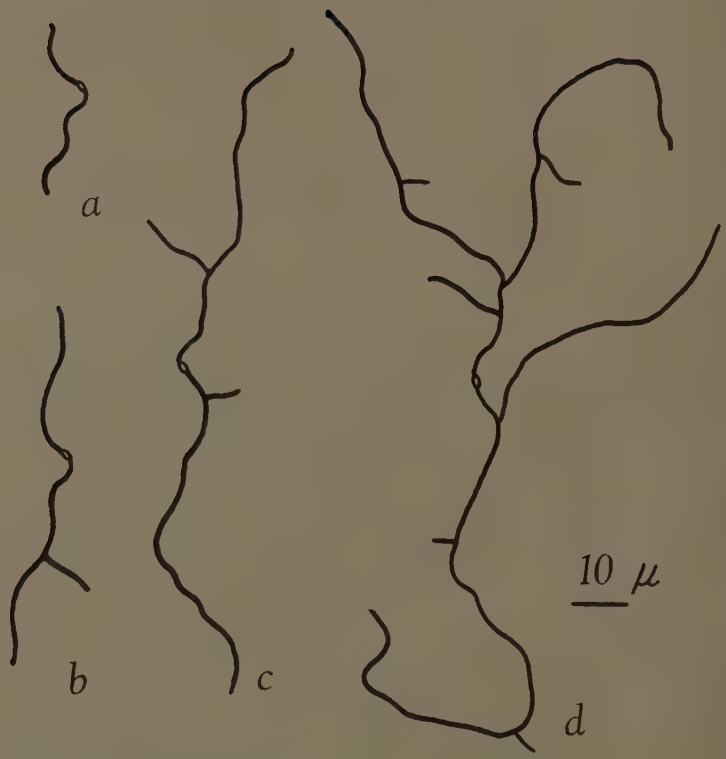


FIG. 1. Unidentified species 1-Sch.: *a*, 9 hours after inoculation; *b*, 13 hours; *c*, 17 hours; *d*, 22 hours

FIG. 2. 1-Sch. (*continued*): *e* is the same as *d* of Figure 1, after having been kept twelve hours longer at a temperature of 15° C.

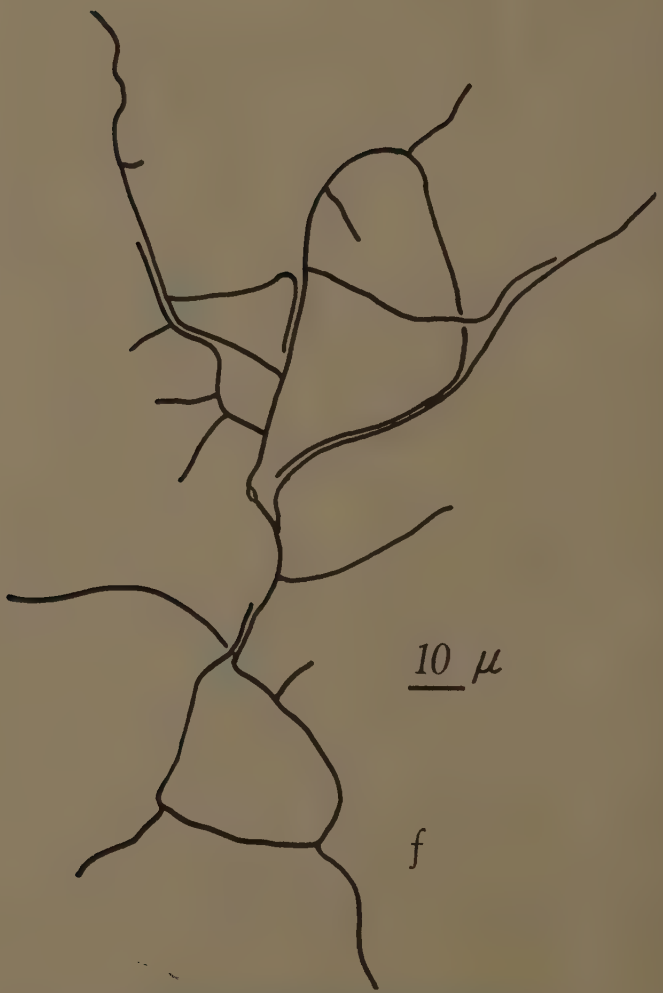


FIG. 3. 1-Sch. (*continued*): *f* is the same as Figure 3, after having been kept five hours longer

FIG. 4. Unidentified species 21–11, Study A: *a*, 27 hours after inoculation; *b*, 30 hours; *c*, 32 hours; *d*, 33 hours

FIG. 5. Unidentified species 21–11, Study A (*continued*), *e*, 34 hours after inoculation

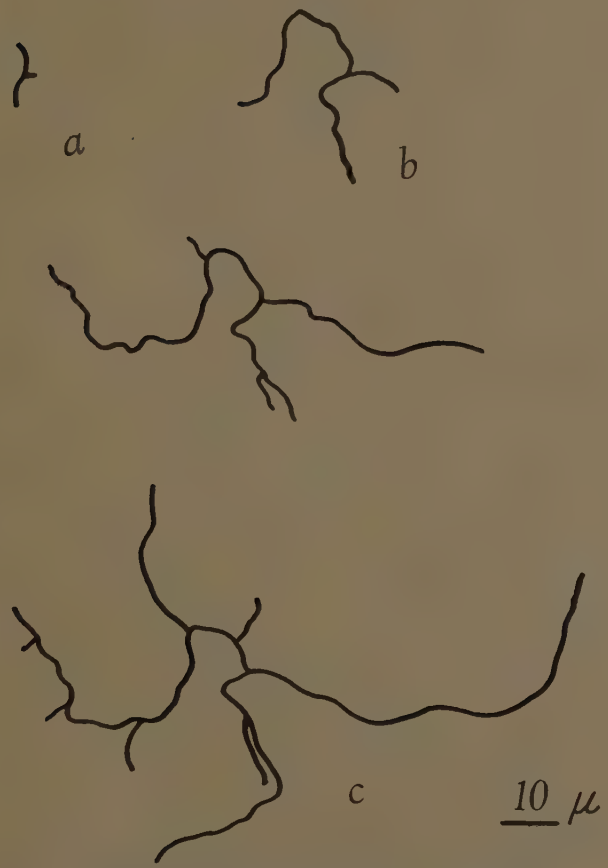


FIG. 6. Unidentified species 21–11, Study B: *a*, 20 hours after inoculation; *b*, 22 hours; *c*, 30 hours

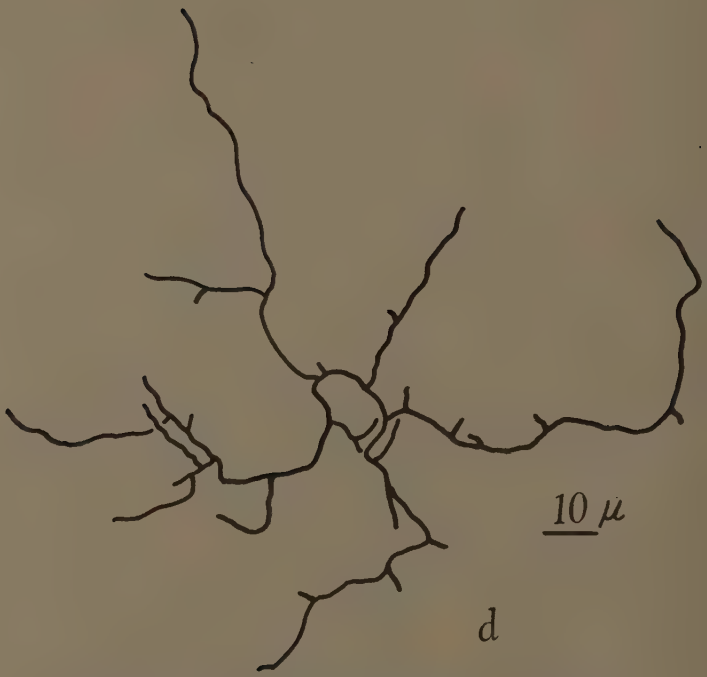


FIG. 7. Unidentified species 21–11, Study B (*continued*): *d*, 55 hours after inoculation

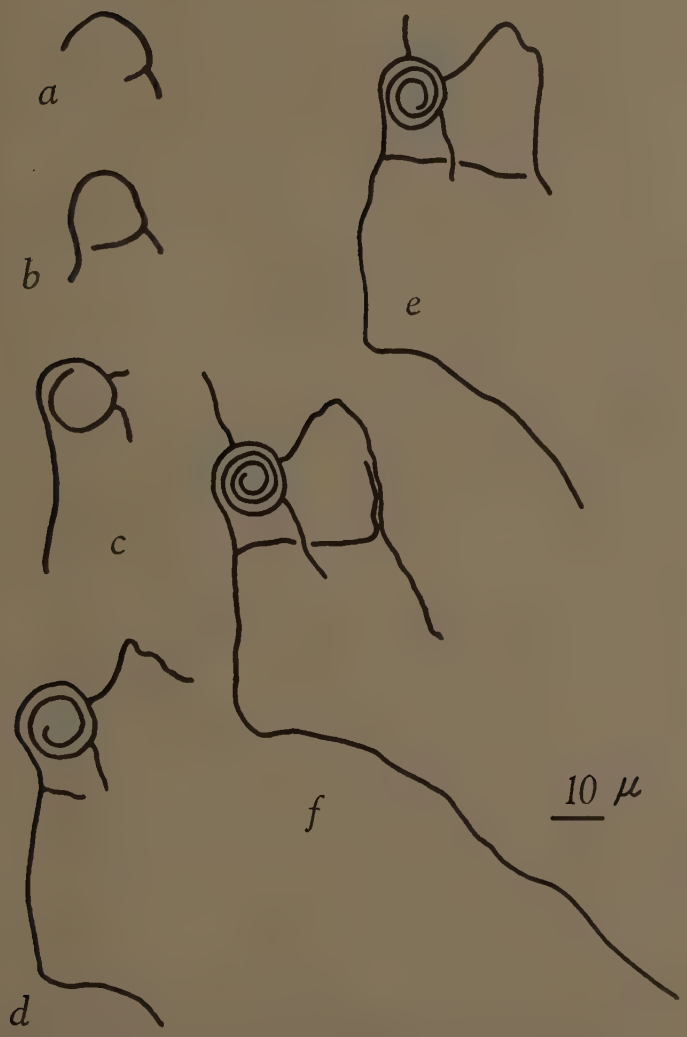


FIG. 8. Unidentified species 21–11, Study C: *a*, 27 hours after inoculation; *b*, 28 hours; *c*, 30 hours; *d*, 32 hours; *e*, 33 hours; *f*, 34 hours

FIG. 9. Unidentified species 21–3: *a*, 21 hours after inoculation; *b*, 25 hours; *c*, 31 hours; *d*, 33 hours; *e*, 41 hours

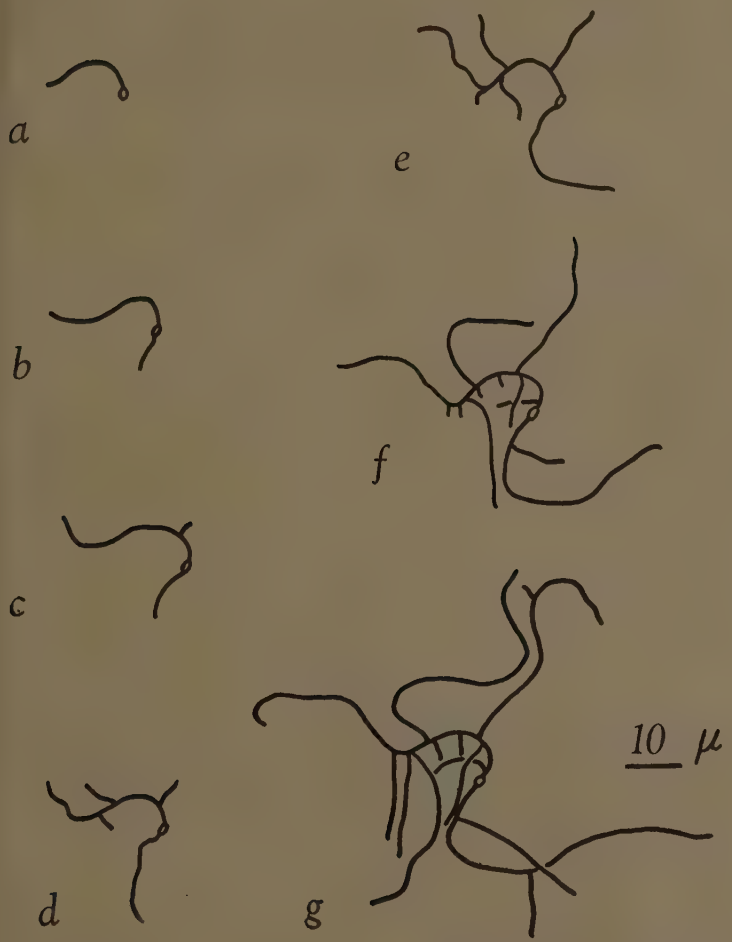


FIG. 10. *Streptomyces griseus: a,* 23 hours after inoculation; *b,* 26 hours; *c,* 27 hours; *d,* 30 hours; *e,* 33 hours; *f,* 37 hours; *g,* 44 hours

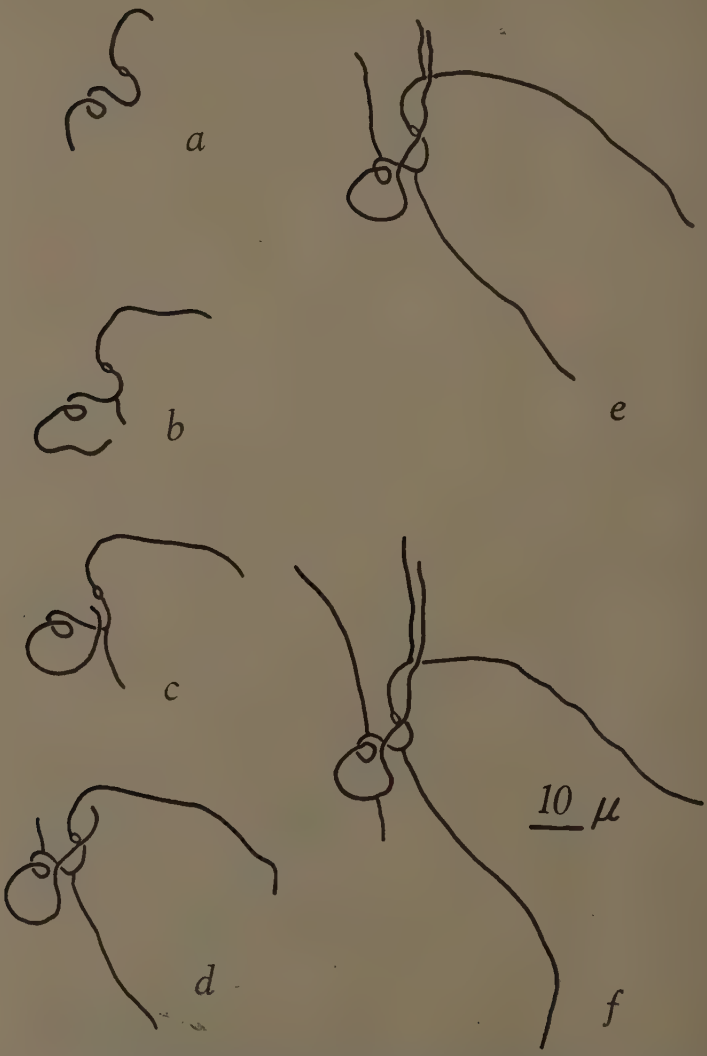


FIG. 11. *Streptomyces lavendulae: a,* 18 hours after inoculation; *b,* 20 hours; *c,* 21 hours; *d,* 22 hours; *e,* 23 hours; *f,* 24 hours

INHERITANCE IN *CUCURBITA PEPO**

EDWIN B. MAINS

CUCURBITA PEPO includes certain of the squashes, pumpkins, and gourds. During the war, when the writer was responsible for courses in applied botany and genetics at the University of Michigan, squashes and gourds were used for class purposes, and the selfs and crosses produced certain characters which have been studied for inheritance.

YELLOW SEEDLING

In the progeny of a self derived from a cross between varieties of summer squash, seedlings occurred which lacked chlorophyll. These were light yellow and died within two or three weeks. The character appears to be similar to that known as luteus in maize. In the progeny of the self there were 71 yellow and 230 green seedlings. In subsequent years progenies from selfs of heterozygous individuals gave ratios as follows: 192 yellow to 579 green; 18 yellow to 60 green; 26 yellow to 89 green; 33 yellow to 85 green seedlings. The totals are 340 yellow to 1043 green seedlings. This ratio is very close to the ratio of 345.75 : 1037.25 expected for one heterozygous pair of factors (Dev. 5.75, P.E. 10.85).

ROSETTED LEAF

A modification of the leaf blade (Fig. 1) which is here designated as rosetted leaf was first noticed in the F_2 of a cross between a summer squash and a gourd. Plants showing this character have the lower lobes of the leaf blades developed inward in a slight spiral giving an effect more or less like a rosette. The character shows considerable variation in its expression and is not always easy to classify. An examination of the parental lines resulted in the discovery that the character occurred in some plants of the gourd parent. In the F_2 of the cross 17 plants were classified as having rosetted leaves and 68 as having nonrosetted.

A cross was made between one of the plants with rosetted leaves (Fig.

*Paper from the Department of Botany and the Herbarium of the University of Michigan. Facilities for growing the lines and crosses were furnished by the Botanical Garden.

1) and a summer squash variety which does not have rosetted leaves (Fig. 2). The plants of the F_1 all developed nonrosetted leaves. A selfed plant of the F_1 gave 55 plants with rosetted leaves and 220 with nonrosetted.

A cross was also made between a plant of the gourd having rosetted leaves and a plant of a white-disk summer squash with nonrosetted leaves. All the plants of the F_1 developed nonrosetted leaves. A selfed plant of the F_1 gave an F_2 having 26 plants with rosetted leaves and 70 with nonrosetted. The three segregating populations produced totals of 98 plants with rosetted leaves and 358 with nonrosetted, which is close to the ratio 114:342 expected for a single pair of heterozygous factors (Dev. 16, P.E. 6.24).

HARD RIND OF FRUIT

In *Cucurbita pepo* the fruits of the gourds and some of the varieties of squash have a hard rind due to thick-walled stone cells of the outer mesocarp. In varieties of squash with a soft rind the walls of the cells of the outer mesocarps of the fruits are thin. A study of the inheritance of these characters was made in crosses given in Table I. Gourds A and

TABLE I

INHERITANCE OF HARD RIND IN THE F_2 OF CROSSES OF CUCURBITA PEPO

Cross	*Hard rind*	*Soft rind*
Gourd A × White Disk	126	52
Gourd A × Yellow Disk	53	20
Sweet Potato × Gourd A	50	16
White Disk × Crown Gourd	76	28
Prolific Straight Neck × White Disk	53	19
Sweet Potato × Prolific Straight Neck	81	30
Total	439	165

Crown and Prolific Straight Neck squash have hard rinds, and the three varieties of squash, White Disk, Yellow Disk and Sweet Potato, have soft rinds.

In all the crosses the fruits of the plants of the F_1 had hard rinds. The accompanying table gives the results obtained in a study of the F_2 of each cross. The ratio of 439:165 is close to the ratio of 453:151 expected for a single pair of heterozygous factors (Dev. 14, P.E. 7.18).

COLOR PATTERN OF FRUIT

The gourd which is designated here as Gourd A has a bicolored pattern (Figs. 3–4), the fruit usually having green and orange-yellow transverse zones. The relative proportions of the zones vary considerably even on the fruits of a plant. Usually there are two zones, but occasionally more than two occur. Some fruits may be mostly green, with only an orange-yellow blotch (Fig. 3). In extreme variations the fruits may be all green (Fig. 4) or all orange yellow. In addition to the bicolored condition, there is a longitudinal striping in which the color of the stripe, either green or yellow, is of a lighter intensity than the ground color (Figs. 3–4).

Gourd A was crossed with a summer squash, variety Zucchini, which is entirely dark green (Fig. 5). The F_1 plants usually produced fruits which were bicolored and without longitudinal stripes (Fig. 5). Fruits of plants showed considerable variation of the bicolored condition. Fruits with definite zones, green except for an orange-yellow blotch, and all green, frequently occurred on a plant. The two latter conditions were more common in these plants than they had been with the parent, and in some plants they were the only conditions. No plant was noted which had all yellow fruits.

The F_2 obtained from selfed plants of the F_1 produced plants with fruits as follows: 162 bicolored without stripes, 53 bicolored with stripes, 28 yellow without stripes, 3 yellow with stripes, 103 green without stripes, and 33 green with stripes (Fig. 6). It is evident that longitudinal striping is inherited independent of the bicolored condition. The F_2 produced 89 plants having longitudinally striped fruits and 293 without striping. This is very close to the ratio of 95.5 : 286.5 expected for a single pair of heterozygous factors (Dev. 6.5, P.E. 5.71).

Sinnott and Durham[1] have reported in their studies that two pairs of factors are responsible for the inheritance of color of fruits in *Cucurbita pepo*. They find that the factor W is epistatic to Y, WY and Wy producing white fruits, wY yellow, and wy green fruits. Two types of striping are discussed. One is considered to be due to factors interacting with color factors to inhibit the expression of the epistatic factors in the areas of the stripes. Whether the stripes are yellow or green is dependent on the genotypes involved. They decide that plain white is dominant over

[1] Sinnott, Edmund W., and Durham, George B., "Inheritance in the Summer Squash," *Journ. Heredity*, 13 (1922): 177–192.

white with green stripes with a single factor difference involved. They were not able to reach any conclusions concerning the relation of white with yellow stripe to plain yellow except that it apparently is dominant. In the other type of striping reported by Sinnott and Durham the stripes are of the same color as the body but deeper in shade. They consider that such stripes are probably produced through the effect of "the striping factor on those factors modifying the intensity of body color." This would imply that the factor involved is believed to be the same as that in the first type of striping. This would be expected to produce green stripes in the yellow portions of Gourd A. It would therefore appear that the factor for longitudinal stripes in Gourd A is different, operating directly on the body colors.

The inheritance of the bicolored condition when studied separately from striping gives a ratio in the F_2 of 215 plants having bicolored fruits to 31 having yellow, and 136 having green. The occurrence of plants with all yellow fruits in the F_2 of the Gourd A cross suggests that the bicolored condition may be due to more than one pair of factors. The extreme variability of the bicolored condition makes it very difficult, however, to reach a conclusion. Some of the plants included in the bicolored class produced all-yellow fruits together with bicolored fruits. Since the plants included in the yellow class each produced only one fruit, their identity and accuracy of classification are questionable. The same is true of single-fruited plants placed in the green class. It is possible that a single dominant factor is responsible for the bicolored condition and that the variability of its expression is responsible for the deviation from the ratio which would be expected.

University of Michigan

EXPLANATION OF PLATE I

Inheritance in *Cucurbita pepo*

Fig. 1. Leaf showing rosetted condition

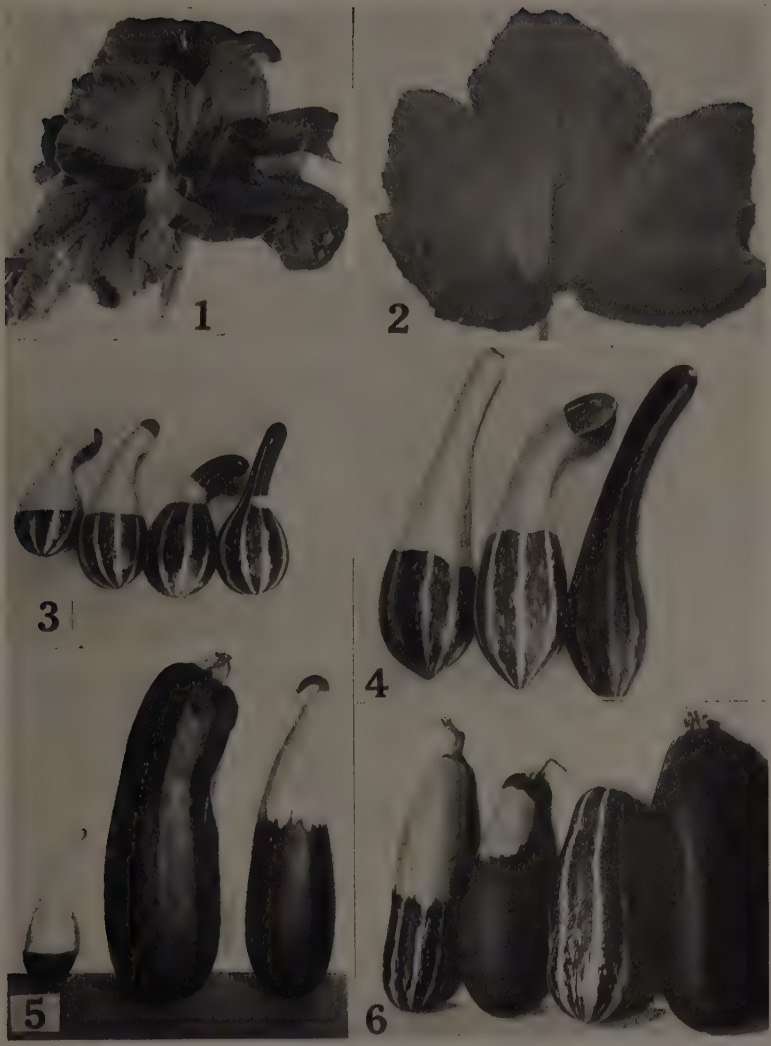
Fig. 2. Leaf of a type commonly found in *Cucurbita pepo;* nonrosetted

Fig. 3. Four fruits taken from a plant of Gourd A, showing variation in pattern

Fig. 4. Three fruits taken from a plant of Gourd A. Note that the one to the right is entirely green

Fig. 5. Fruit to the left from Gourd A parent, middle fruit from Zucchini parent, fruit to the right from a plant of the F_1 of the cross Gourd A $\times$ Zucchini

Fig. 6. Some of the types found in the fruits of the F_2 of the cross Gourd A $\times$ Zucchini, reading left to right: bicolored with longitudinal stripes, bicolored without stripes, green with longitudinal stripes. All-yellow fruits with and without stripes were also obtained



Inheritance in *Cucurbita pepo*

REPRODUCTION OF *ACROSYMPHYTON CARIBAEUM**

WM. RANDOLPH TAYLOR

DURING the spring of 1949 the writer undertook at Bermuda certain morphological studies of marine algae and also made a general survey of the algae about the islands. Since some peculiarly interesting Rhodophyceae not readily available on the mainland were accessible there, these received his first attention.

Acrosymphyton has been separated from Dudresnaya on the basis of special features of the carpogonial apparatus of *A. purpurifera*. It was known (Sjöstedt, 1926) that *D. caribaea* should accompany *D. purpurifera* into the genus Acrosymphyton, because of the position of the auxiliary cell, but the development of its reproductive structures has not previously been made the subject of careful research and, since this plant was found at Bermuda (although rare), advantage was taken of the opportunity to make a thorough study of it, so that it could be compared with *A. purpurifera*, the only species so far completely studied. Through the courtesy of the curator at the New York Botanical Garden, Dr. D. P. Rogers, the writer was able to review the Collins and Howe specimens; and Dr. W. L. White, of the Farlow Herbarium, kindly loaned plants collected by Hall and Farlow. This has permitted considerable correction of herbarium determinations of plants of these two genera, respecting the American records.

One of the notable species of Rhodophyceae reported as among the features of the Bermudian flora is *Acrosymphyton caribaeum*. The plants are bushy, with prominent leading and secondary axes reaching a height of 16 cm. or more, though commonly less. The branching is

*Contribution from the Department of Botany, University of Michigan, No. 917, and from the Bermuda Biological Station for Research, No. 163.

This work was facilitated by a grant from funds placed at the disposal of the Bermuda Biological Station by the American Philosophical Society. For this generous aid, and for the very cordial coöperation of the former director of the Station, Dr. D. E. S. Brown, and of his assistant under the grant, Mr. Albert J. Bernatowicz, the writer is exceedingly grateful.

rather regularly radial, of 5–6 successive degrees. Reported distichous branching is probably an artifact produced by flattening these highly gelatinous specimens for drying or the result of a slight occasional tendency to fasciation. The main axes may reach a diameter of 5–8 mm., but are usually much less; the ultimate ramuli are generally exceedingly slender, one millimeter or less in diameter, long and sharply tapering. In color they are dull when living, but when dried are a stronger rose red. This plant has been found at but a very few stations, where it seems to have the same growth habits as *Dudresnaya crassa.*

Acrosymphyton caribaeum was represented in the herbarium of the New York Botanical Garden by five specimens under the name *Dudresnaya caribaea.* One, from Bermuda, was sterile; three from Dry Tortugas, Florida, and one fragment from Miami Beach, Florida (of which the major portion was in the writer's herbarium), were confirmed as *A. caribaeum.* To these must be added ten erroneously placed in *D. bermudensis* (including two issues of Phyc. Bor.-Amer. *no. 2195*), all Bermudian except one from Great Bahama Island. Since the two Garden copies of the Phycotheca specimens, one of which was Collins' own, and those in the sets belonging to the University of Michigan and the writer are incorrectly identified, the implication is that all specimens of Phyc. Bor.-Amer. *no 2195* are to be mistrusted.

It is necessary to remark here, parenthetically, that the observation made above regarding the misidentification of specimens labeled *"D. bermudensis"* does not imply any invalidity in the species itself. A small specimen in the Collins herbarium labeled "Dud #2" (in pencil) and *"Dudresnaya bermudensis* from the type material" closely resembles the photograph of Setchell's type plant, and when examined microscopically conforms to his definition in the essential points of peripheral filaments and auxiliary branch. Presumably it comes from the Farlow material of 1881. While the vegetative filaments of *D. bermudensis* resemble those of *A. caribaeum,* the reproductive structures clearly show that the relationship is with *D. crassa.* Setchell's description (1912, p. 244) does not seem to the writer to be correct, for he states that "From *D. crassa* it differs . . . [by] the absence of a single specialized (smaller) auxiliary cell in each auxiliary branchlet." Material properly expanded with a solution of caustic potash showed that the auxiliary cell was decidedly smaller than the neighboring cells, which reached 15 μ diam., though possibly the whole branch was shorter and much blunter, and the cell distinctions somewhat less than those in *D. crassa.* The obovoid cells

of the peripheral filaments decreased for the outer 3–4 divisions; in the cells near the surface the diameter was 5.4–7.5 μ.

Acrosymphyton caribaeum was not as abundant in 1949 as was *Dudresnaya crassa,* but excellent fertile material was eventually found on one occasion, as well as a very few sterile plants. In branching, in gelatinous character, and in general structure there was little to distinguish these plants from those of Dudresnaya. Perhaps in young plants there was more difference in diameter between the ultimate and the main branches, and the young branches probably tapered to more delicate tips, but in old specimens this was not evident. In both the basic structure consists of a series of very large axial cells, each bearing somewhat above the middle at first two, later four, repeatedly branched vegetative ramuli, completely enveloping the axis. The axial cells in our material reach a diameter of at least 60–130 μ; they are supplemented by slender (7.5 μ) rhizoidal outgrowths from the lower cells of the vegetative ramuli. These ramuli branch repeatedly, depending on the age of the part examined, and the cells are progressively supplied with more chromatophores as one approaches the surface. At the time that reproductive structures are forming they have subdichotomously forked 5–7 times at moderate angles, the cells rather more elongated in the lower series and often subfurcate on the end, but the cells toward the surface are broadly obovate and about 6.5–10.0 μ diam. (Fig. 4).

The irregularly rounded spermatangial clusters develop abundantly on the outer divisions of the vegetative branchlet systems in male plants, replacing the ultimate divisions. Branching here is no longer dichotomous, but irregular to subopposite (Figs. 1–3).

Carpogenic branches were not difficult to find, though less abundant than in *Dudresnaya crassa.* The difficulties lie in interpreting them when they are found, for their growth habit is very likely to obscure the important characters. They first appear as a short row of cells near the base or a vegetative branchlet, as a division of a dichotomy or a trichotomy. They are distinguishable by failure to fork immediately like the vegetative ramuli; the cells remain short. The little initials, when about 5–7 cells long, begin to curve, and may show signs of developing side branchlets of their own (Figs. 5, 10). With growth the curvature becomes greater, and the side divisions curve inward. Except near the carpogonium and near the base each cell may have an opposite pair of these, which become 3–4 cells long (Figs. 6–8). The carpogonium is at first simply oval; later the trichogyne becomes more narrow and elon-

gates, while the curvature further increases (Figs. 6–11). The whole structure is so crowded and confused by these curvatures that it is only the exceptionally well-flattened carpogenic branch which can be used for an illustration. The figures given are by no means average in this respect; they are particularly clear selected examples. The trichogyne, at first pointed down the branch, eventually curves outward toward the surface of the plant.

Fertilization is promptly evidenced by the more wrinkled aspect of the trichogyne and the appearance of a connecting outgrowth or primary oöblast from the carpogonium. This is turned or soon swings down the inner face of the carpogenic branch (Figs. 12–13). In its progress it fuses with one or more of the terminal cells of the side ramuli. The terminal cells are little differentiated, being merely rounded and somewhat larger than the others. These cells are doubtless nutritive in function, rather than auxiliary ones destined to produce cystocarps; in rare instances (Fig. 15) one of them by its isolation and size suggests that it is actually a potential auxiliary. No examples of effective functioning of such aberrant auxiliaries were observed. After the initial fusion of the outgrowth from the carpogonium, extension and further fusions occur (Figs. 14–16). At least three or four of these end cells, as well as others, may become involved. It was occasionally noted that, in addition to the lateral ramuli from the carpogenic branch, one-celled outgrowths could develop from the inner face of these laterals, and from the axis itself, and could become involved (Fig. 11). As the process advances, the cell contents become less dense, and eventually the whole seems impossible of interpretation, even by the use of stains. Fortified by the fusions on the carpogenic branch, one or more true oöblasts are produced which strike out in various directions from the fusion mass, potentially to connect with auxiliary cells at some distance in the plant, and to initiate carpospore formation (Fig. 15).

The auxiliary cells in *Acrosymyphyton caribaeum* are terminal on their axes, and when mature are quite distinct, but large and with more sharply defined walls rather than especially dense with stored food. Axes arise on the lateral vegetative ramuli, generally equivalent to one side of a fork. The other, vegetative, side far outstrips them before their identity can be distinguished (Fig. 18). Then their short, stout, rather dense cells mark them out. With subsequent growth of the vegetative ramuli additional auxiliary axes may be produced (Figs. 19–20) until there may be several. The length varies much, the functional axes having from

5 to 12 cells (Figs. 20, 28), but doubtless more extreme examples could be found. The diameter is about 8–12 μ; that of the terminal auxiliary cell, about 12–14 μ. The auxiliary axes are typically unbranched, but occasionally lateral branchlets are seen which have no special function (Figs. 21, 23). Division of the axes into several functional branches is not rare. As many as seven potential auxiliaries were seen on one axis (Fig. 22), and numerous cases were noted in which more than one of these could function (Fig. 17). Generally the picture was then so confused that no reproducible drawings could be made.

The true oöblast, on making contact with an auxiliary, seems generally to attach and fuse with the side of it. The auxiliary promptly elongates axially, the bulk of the cytoplasm passes to the distal end, and the oöblast grows out again from the point of contact to continue toward other axes (Fig. 26). It was quite possible to follow these succeeding contacts and fusions. We may have them between auxiliaries on the same forked axis (Fig. 17), where one has already formed carpospores while the other has only begun, or, more commonly, with relatively distant auxiliary axes (Figs. 24, 25) where the bridging oöblasts usually remain to show the connection. Though not figured, the oöblast from the fusion cell in Figure 16 was traced through four attachments to independent auxiliary branches, the first and fourth producing normal cystocarps but the other two seemingly sterile. It proceeded yet further in the plant. Cross walls in the oöblasts were generally formed some distance behind a point of fusion, and eventually in the extension at a similar distance, but were by no means consistently discernible.

The cystocarp is initiated from the protoplasm-rich elongated upper part of the auxiliary fusion, where a cell is separated by a cross wall close above the level of the oöblast attachment. This cystocarp initial cell is thus distinctly denser than the rest of the structure, which contains little protoplasm. The subsequent irregular divisions (Fig. 27) produce a relatively small mass of large dense carpospore cells (Figs. 17, 28). The further history in this plant is uncertain. As in *Dudresnaya crassa*, tetrasporangial plants are unknown, and there is no morphological clue to the occurrence of meiosis in any definite alternative place. Critical cytological work is needed in both instances to show the true nuclear conditions, and this will be difficult, though not impossible, because of the gelatinous nature of the species.

Our first substantial account of the reproductive apparatus of Acrosymphyton appears in the work of Bornet and Thuret (1867, p. 156) on

A. purpurifera (as Dudresnaya). They correctly portray carpogenic and auxiliary branches. They also recognize, if a bit imperfectly, a primary fusion within the carpogenic branch and communication by slender filaments between this and successive auxiliary cells, with subsequent cystocarp formation. The delineation of structures is, as one would expect from Édouard Bornet, exquisite. Schmitz (1883, p. 255) and Berthold (1884, p. 12; pl. 5, fig. 1) add nothing to these microscopic observations, but the latter figures the plant excellently. Oltmanns (1898, p. 101) reported on stained material, and so his figures show some distortion; his comprehensive text (1922, p. 387) adds nothing of moment. More clearly than his predecessors he recognized the morphology of the primary fusions on the carpogenic branch and formulated ideas still current regarding the transfer of nuclei to the auxiliary cells, but he did not take up the problem, so important here, of chromosome reduction in the general absence of tetrasporic plants. Sjöstedt (1926, p. 8) recognized the importance of the differences between these reproductive structures and true Dudresnaya by segregating in Acrosymphyton the species *purpurifera* and *caribaea*. The present study shows the general similarity between these two species, though some differences appear. Kylin (1930, p. 22; 1937, p. 211) gives a new set of figures, but his description follows the established line. The great disproportion which appears between carpogenic branch and auxiliary filament in *A. caribaea* does not appear in *A. purpurifera*, and the auxiliary branches which he figures as of 5–6 cells are certainly much shorter than those of *A. caribaea*. Feldmann (1942, p. 236) confirms some points respecting *A. purpurifera*, but adds no new data. Oltmanns noted development of three connecting outgrowths from the carpogonium, one fusing with the end cells of each lateral set of branchlets and the third with superficial cells near the axis, though this one might be absent. We generally find only one connecting outgrowth in *A. caribaea* (Fig. 4), though sometimes there are two (Fig. 7), but no more, and in no case are they cut off by a cross wall at their point of origin, as Oltmanns and Kylin clearly figure for *A. purpurifera*. The one or, occasionally, two outgrowths characteristic of *A. caribaea* initiate a large general fusion cell on the concave side of the carpogenic branch, without cross walls, instead of the compartmented structures which he figures. In both species of Acrosymphyton there are few, usually one or two, oöblasts formed from each carpogenic branch, and few secondary oöblasts from the points of junction with auxiliaries. Espe-

cially in the first feature this is very different from the condition in *Dudresnaya crassa.*

University of Michigan

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EXPLANATION OF PLATE I

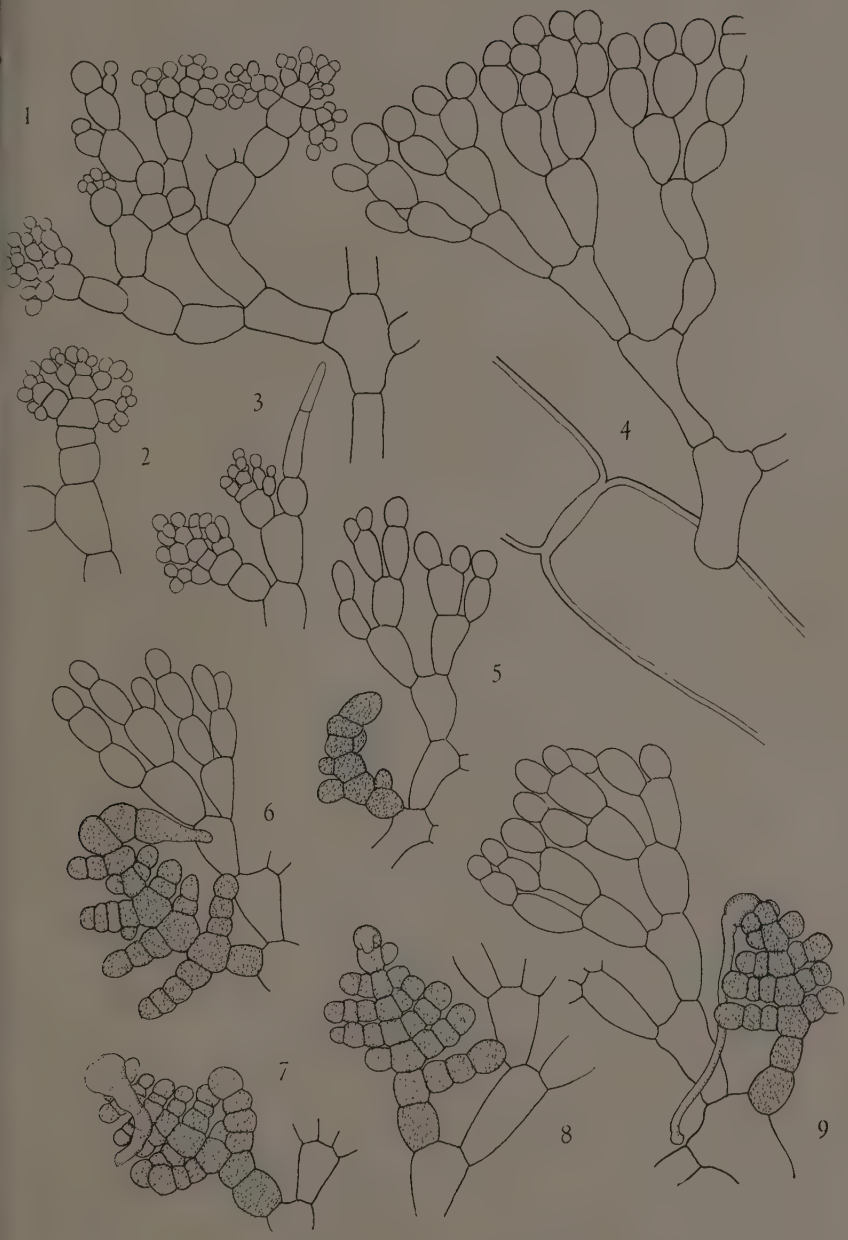
Acrosymphyton caribaeum

(All figures × 575)

FIGS. 1–3. Tips of assimilatory branches bearing clusters of spermatangia

FIG. 4. Well-developed assimilatory filament cluster on an axial cell, previous to the formation of secondary longitudinal filaments

FIGS. 5–9. Stages in the development of carpogenic branches, shown attached to the lower cells of young assimilatory filaments. In Figure 5 lateral ramuli have just begun to appear and the carpogonium is undifferentiated, but the axis is already curved. Figures 8, 6, 7, 9 show successive increases in the development of the lateral ramuli and elongation of the trichogyne



Reproduction of Acrosymphyton

EXPLANATION OF PLATE II

Acrosymphyton caribaeum

FIG. 10. Relatively young carpogenic branch, the trichogyne well developed but the lateral ramuli rudimentary. × 575

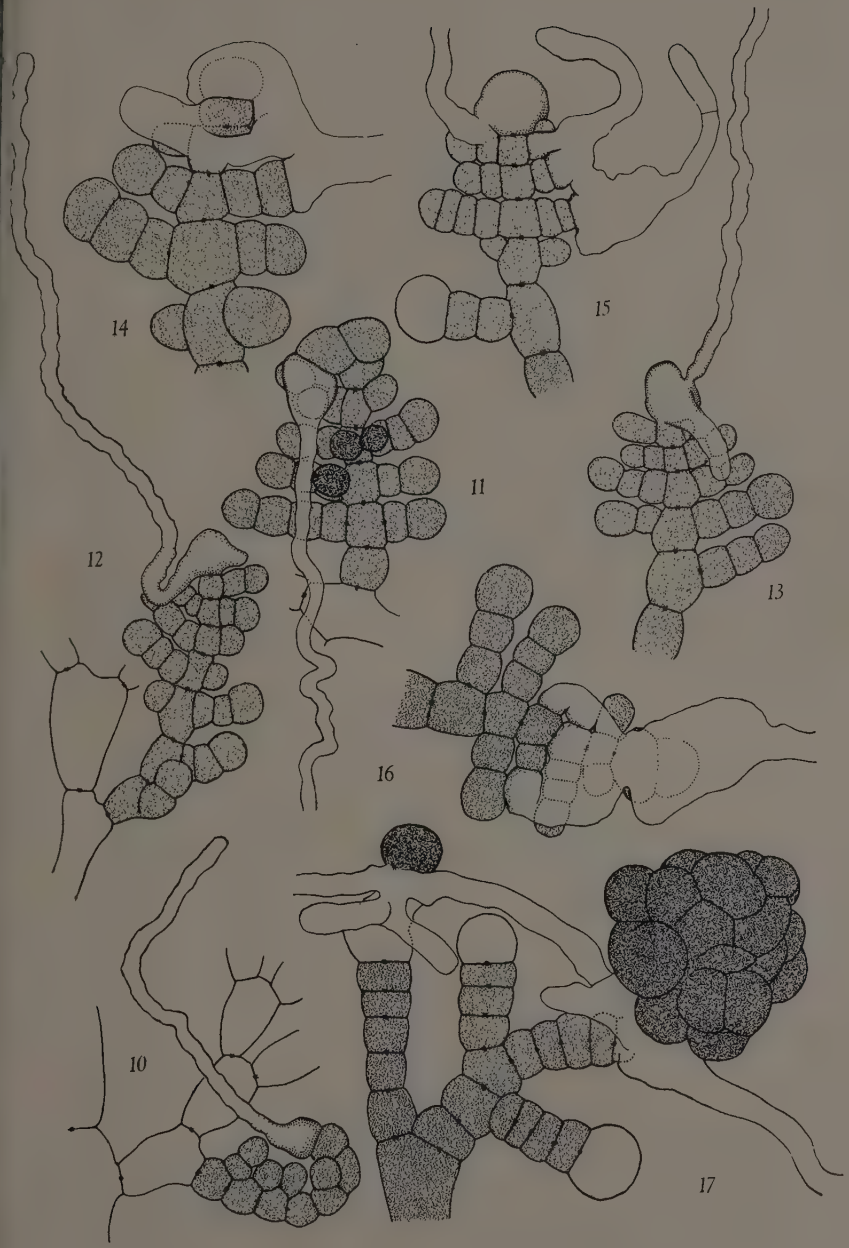
FIG. 11. Mature carpogenic branch. On the face of the branch are shown certain special cells (three darker-shaded, two more under the carpogonium and shown in outline only) formed at right angles to the plane of the lateral ramuli. × 1000

FIG. 12. Carpogenic branch after fertilization. The initial of the connecting outgrowth appears as a prolongation of the right-hand angle of the carpogonium. × 755

FIG. 13. Carpogenic branch after fertilization. The outgrowth runs down the face of the branch. × 755

FIGS. 14–16. Examples of the fusion of the connecting outgrowth with nutritive cells of their respective carpogenic branches. While it is usually the enlarged terminal cells of the ramuli which become involved, one notes in Figure 14 fusion with an axial cell, and it is quite probable that more than terminal cells are involved in Figure 16. In Figure 15 a lower cell of the carpogenic branch bears what appears to be a true auxiliary cell. Figure 14, × 752; Figures 15–16, × 1000

FIG. 17. A branched auxiliary ramulus, showing two of the four auxiliary cells activated. The oöblast after fusing with that on the right has initiated another cystocarp, which is still in the one-celled stage, on the left. × 725



Reproduction of Acrosymphyton

EXPLANATION OF PLATE III

Acrosymphyton caribaeum

(All figures × 575)

FIGS. 18–20. Stages in the development of auxiliary branches on assimilatory filaments. As Figures 18–20 show, there is commonly a succession in one assimilatory cluster. The terminal unshaded cell is the mature auxiliary

FIGS. 21–22. Auxiliary branches which bear lateral ramuli. In Figure 21 they appear to be sterile, but in Figure 22 all seven apices appear to bear potentially fertile auxiliaries

FIGS. 23–25. Auxiliary cells to which oöblast filaments have recently fused

FIG. 24. Formation of the first initial cell of the cystocarp. This branch was directly connected by the same oöblast with that shown in Figure 25

FIG. 26. Formation of the initial cell of a cystocarp

FIGS. 27–28. Stages in the formation of the cystocarp

Reproduction of Acrosymphyton

VASCULAR DEVELOPMENT AND TRANSITION IN *ECHINACEA PURPUREA*

JAMES WILLIAM UNGER

INTRODUCTION

ECHINACEA PURPUREA (L.) Moench is a member of the Compositae, series Tubuliflorae, tribe Heliantheae. A considerable amount of morphological work has been done upon members of the Compositae in relation to the flower ontogeny, the type of megagametophyte, the embryo development, and the vascular transition in the seedling. There are, however, few accounts of embryogeny and seedling differentiation within a given species. Miller and Wetmore (1945) traced the ontogenetic development of *Phlox drummondii* from the megagametophyte through the differentiation of the seedling and the maturation of vascular elements. The present paper is part of a morphological study of the development of a species of Echinacea from the origin of the floral parts through seedling development and vascular transition.

Esau (1943) summarized the early vascularization of embryos and seedlings with the conclusion that, while much work has been done on the development of the embryo, few investigators have been concerned with the manner in which the early vascular system of the embryo is blocked out. Nast (1941), in her paper on *Juglans regia*, explained that vacuolation of the cells in the pith and cortex of the hypocotyl and root delimits the future vascular regions of embryos even before the cotyledons are present as separate structures. Phillips (1937), working on Cynara seedlings, concluded that early vascular tissue appears near the base of the cotyledons and differentiates acropetally and basipetally from that level into the hypocotyl and the upper cotyledons. Miller and Wetmore (1945), in a study of Phlox embryos, found that the xylem appears first in the cotyledons and matures down into the hypocotyl and up into the cotyledons; the phloem differentiates in a similar manner but appears later than the xylem.

Papers are available dealing with vascular transition in seedlings of the Compositae, beginning with the work of Van Tieghem in 1870. Lee

(1912) studied seedling anatomy in about fifty species of the Compositae. Havis (1935) traced the transition from root to typical stem structure in *Tragopogon porrifolius*. Siler (1931) worked out the account of vascular transition in the seedling of *Helianthus annuus* and *Arctium minus*. Similarities may be noted in the development of these species, but it is difficult to state definitely a specific method of transition which is constant for the Compositae as a family.

MATERIAL AND METHODS

The floral buds of the purple cone flower and stages from flower to mature seed were collected from the arboretum of the University of Wisconsin during the months of July, August, and September, 1947. The material was fixed in formal-acetic-alcohol and in Craf's modification of Nawaschin's solution. Mature seeds were stored under refrigeration as a means of preservation and were germinated upon wet filter paper in petri dishes. Seedlings of different ages were selected for fixation, were dehydrated by a butyl alcohol series, and imbedded in paraffin (58°–59° C.). Serial longitudinal and transverse sections were cut at 10–15 microns. Most of the seedlings were stained with safranin and fast green. Root-tip smears were made by the use of aceto-orcein to determine the chromosome number of the plant.

THE DEVELOPMENT OF THE SEED AND SEEDLING

The mature embryo in the seed is uncurved and ranges from 3 to 3.5 mm. in length. The hypocotyl is short, and the cells composing it are unelongated until suitable moisture brings about growth and the fruit coat is cracked. The cotyledons are much longer than the hypocotyl and make up the greater portion of the embryo in the mature seed. No trace of suspensor remains at maturity.

It is possible to assign an approximate stage of development to the young embryo in the immature seed by observing the amount of integumentary tissue persisting. The integument gradually becomes collapsed as the embryo enlarges and the endothelial layer is obliterated. A mature embryo is surrounded by only the outer few cell layers of the integument.

At the time that the embryo has reached a stage of development equal to about two thirds its maximum size in the seed, considerable elongation of two layers of cells beneath the epidermis of the cotyledons indicates an early palisade development. The layers are located on the

abaxial side of the cotyledon and eventually become the photosynthetic tissue on the upper surface of the cotyledon after it emerges from the soil. At this age the hypodermal layer of cells shows an increased number of longitudinal divisions and great elongation in the longitudinal plane that results in a layer of narrow palisade cells. The second layer is not so conspicuously elongated as the upper. The remainder of the cotyledonary mesophyll is a tightly packed region of parenchyma that is somewhat thicker than the spongy tissue of a foliage leaf. The spongy parenchymatous nature of the mature foliage leaf is lacking in the cotyledons, and no stomata are formed in the epidermis at this age.

The earliest indication of vascular differentiation in the immature embryo is noted when it has reached the length of about 700 microns. The cotyledons average 395 microns in length at this stage. A light staining area, which is the first indication of a pith, is prominent just below the unelongated epicotyl. Outside this region and extending up into each cotyledon is a more heavily stained area that delimits the location of the provascular strands. The cells of these strands are less highly vacuolate than the pith cells and those that will contribute to the cortex. The inner layer of the cortical region is composed of cells similar in size to those of the provascular tissue. By tracing the histogens of the root tip from the lower end of the hypocotyl upward into the cotyledon it is possible to follow the line of separation between the cortex and the stele.

An embryo measuring 2.6 mm. in length shows slightly more development of provascular tissue in the cotyledons and the upper hypocotyl, as is indicated by the elongation of cells in a narrow region just within the inner layer of cortex. The cell elongation is slight, but the prominent nuclei and vacuolation in the cells of the provascular tissue further aid in making it distinguishable. In cross sections of the hypocotyl certain strands of the procambium are more sharply delimited than others, and the number varies according to the level in the embryo. The strongly developed strands of the procambium will become the future phloem strands. The xylem strands of the hypocotyl and the cotyledons are much less sharply delimited at this time, and the portion of the procambium from which they will be formed resembles areas of parenchyma that are alternate with the developing phloem through most of the hypocotyl. These become collateral with the phloem of the upper cotyledons in later stages. A pith is present in the upper hypocotyl, and the procambium is in the form of a dissected cylinder. The upper hypocotyl has a provascular cylinder of greater diameter than the lower levels, and three strands

are evident that are continuous with the developing strands in each cotyledon. The endodermal cells are enlarged at this age and are most distinct outside the areas of undeveloped phloem.

Embryos dissected from mature seeds give conclusive evidence of the plan of vascular development. At this time the phloem and xylem show the first sign of maturation. All evidence indicates that the maturation of the first phloem elements in a mature seed first begins near the base of the cotyledons and proceeds acropetally and basipetally from that region. The cell walls in the portion of the procambium from which phloem matures are most distinct at this level, and the nuclei of the cells in these developing phloem areas are large and granular in contrast to those of cells in the hypocotyl, root, and upper cotyledons. The walls of the immature phloem cells fit closely together. Frequently intercellular spaces are present in the cortex outside the phloem, and these spaces are continuous with spaces in the lower root area.

The origin of the protoxylem is more difficult to determine. Immature xylem cells become evident in the mature seed at a level in the lower part of the cotyledons. They may be identified by a decrease in the amount of protoplasm in a few cells of the provascular strand. These early xylem cells are similar in shape to the parenchyma surrounding them, but are distinguishable from the parenchyma by a shrinkage of the cell contents and a thickening of the primary walls. This characteristic has been seen in more than one series and represents the first visible step toward maturation.

In seedlings twenty-four hours after germination has begun the provascular strands in the upper hypocotyl increase in diameter by longitudinal divisions of cells, particularly in the inner portion of the strands. As viewed in transverse section, these divisions are periclinal and result in radial rows of cells. One of the cells in the innermost radial row, at the level of the lower cotyledon, begins to develop a secondary wall thickening, and the primary wall stains deeply. Cells of this type constitute the first mature xylem elements and develop annular and spiral lignified secondary wall thickenings. The nucleus disintegrates during the time that secondary wall formation is going on; in some seedlings this is followed, twenty-four hours after germination, by the complete disappearance of the protoplast. The end walls of these elements are slightly oblique and in close contact with other similar cells in a continuous row. Several fully matured rows of protoxylem and early metaxylem elements were observed near the base of the cotyledons within twenty-four hours

after germination had begun. From this time on the xylem development takes the lead over the phloem, and in forty-eight hours spiral, annular, and scalariform metaxylem elements have matured into the lower hypocotyl and the upper limits of the cotyledons. Elongation of cells occurs just below the cotyledonary node of the seedling, and the procambial cells in this region are longer than those of the cotyledonary strands.

Adjacent to the first xylem elements of the upper hypocotyl the provascular strand continues to divide longitudinally and cuts off linear rows of narrow cells that in turn divide periclinally. Some of these cells, in the outer part of the strand, become enlarged and function as the phloem mother cells. Continued procambial divisions produce additional rows of cells between the xylem and the phloem mother cells that later mature into metaxylem, metaphloem, and cambium. The end walls of the early phloem cells are flattened, and occasional transverse divisions form cells that may again divide periclinally. Observation of one-, two-, and four-day-old seedlings fails to reveal the presence of mature sieve tubes, but this may be accounted for, in part, by the fact that sieve tubes are often comparatively indistinct in the protophloem. The other possibility is that phloem has not matured at this age. Companion cells accompany the sieve tubes in older seedlings, but in seedlings of 24–48 hours it is difficult to be certain whether the accompanying cell is a companion cell or the result of a recent procambial division. Mature sieve tubes were first positively identified by the presence of sieve plates in the cotyledons of eight-day seedlings. The earliest maturation may have occurred in seedlings between four and eight days old. A provascular strand develops acropetally into the first true leaf of eight-day seedlings, and the strand connects with one of the lateral bundles of the upper hypocotyl. At this age it is not possible to distinguish between the portions of this strand that will form xylem and phloem in the leaf.

As determined by chromosome counts made from cells of seedling root tips, the diploid number of chromosomes in *Echinacea purpurea* is twenty-two.

VASCULAR TRANSITION

In seedlings eight days after germination the xylem and phloem strands are sufficiently well matured to enable one to determine their orientation throughout the hypocotyl and the cotyledons. Large parenchymatous cells at a low level in the central part of meristematic root tip show the location of the future metaxylem before the first poles of pro-

toxylem appear. At a slightly higher level in the primary root two patches of cells which will mature into phloem develop. About two millimeters back from the tip the two root poles have each been established by the lignification of one vessel for each pole. Higher in the root the number of vessels increases to two or three, at this age, and the phloem areas are larger. The xylem vessels are five- to six-sided, and spiral or annular thickenings are found on the walls. Many of the larger metaxylem vessels have scalariform thickenings on the side walls. The primary root is diarch and exarch, and the two xylem arms are each made up of four or five vessels that alternate with two lateral bands of phloem (Fig. 1). The phloem is separated from the xylem by several rows of parenchyma, and a number of large cells in the center will later mature into metaxylem. The vascular tissue is bounded on the outside by a single layer of pericycle. At this age two prominent layers of cells bound the inner cortex over the areas of phloem. These cells arose in the embryo during a late stage of seed development by periclinal divisions of the innermost periblem layer. Over the xylem the inner cortical layer has not divided periclinally into two cells but remains one cell thick. Casperian bands, which characterize the endodermis, are located only on the walls on the inner layer of cells. Between the endodermis and next layer of cortex are found conspicuous intercellular spaces that extend far up into the hypocotyl from the meristematic root tip.

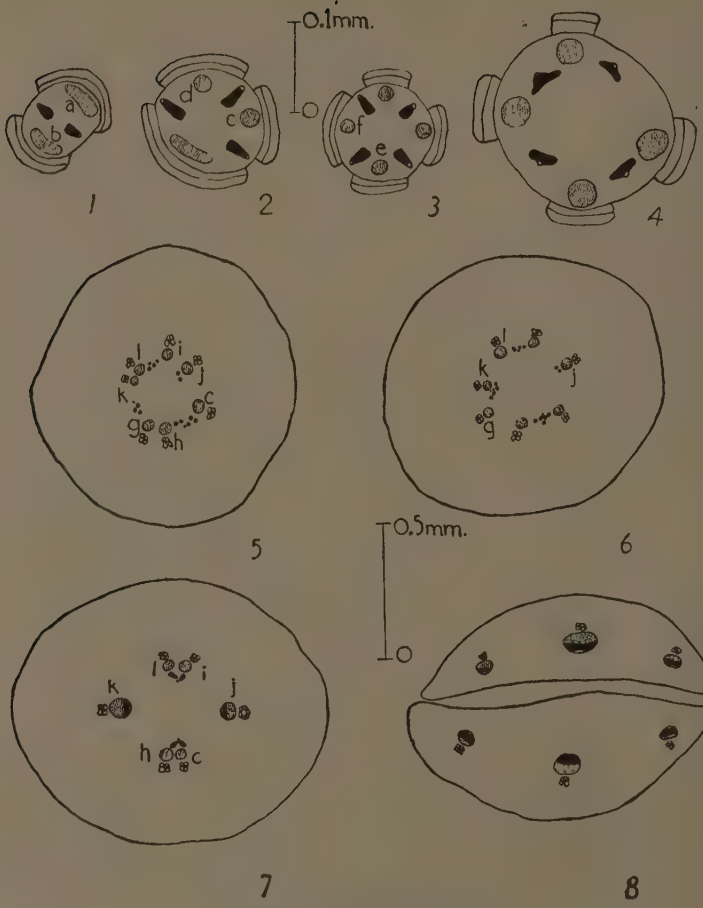
At a slightly higher level in the hypocotyl one of the two phloem areas (Fig. 1*a*) bifurcates into two new groups of phloem (Fig. 2*c, d*), and these groups start to separate from each other. A third exarch xylem arm differentiates radially between the two new groups of phloem (Fig. 2*c, d*). This arm is at right angles to the two original xylem arms of the root. The double arcs of inner cortical cells accompany the phloem groups in origin, so that outside each new phloem group is a separate arc.

At a level in the middle of the hypocotyl the second original group of phloem (Fig. 1*b*) bifurcates, and two new groups (Fig. 3*e, f*) result from the bifurcation. Farther up in the hypocotyl these groups of phloem separate, and a fourth xylem arm originates between them to establish a tetrarch condition (Fig. 3). The cortical arc remains one cell thick over the xylem arms and two cells thick over each group of phloem. Tetrarchy persists as far as the upper portion of the hypocotyl. The hypocotyl, therefore, is largely rootlike in structure. Up to this level the xylem is exarch and radially alternate with the phloem. Many pericycle cells at this level have very large nuclei and indicate clearly the possible origin of

secondary roots from the pericycle. The young branch-root primordia arise from the pericycle at different levels in a somewhat cyclic arrangement. An interesting point was noted in connection with this observation. Each primordium seems to be connected with the next one above in the hypocotyl by a series of pericyclic cells containing nuclei like those of the primordia. These nuclei are markedly larger than those of the usual pericycle cells.

The upper hypocotyl has a pith of greater diameter than the lower hypocotyl. The transition from root to stem structure is completed within the upper half of the hypocotyl. During this change of vascular orientation the metaxylem elements are differentiated laterally by a gradual "migration" at higher levels to each side of the protoxylem (Fig. 4). The vessels in each lateral group are closely associated at first and become separated from one another by parenchyma at a higher level. Two of the phloem groups (Fig. 2*d;* Fig. 3*e*) bifurcate at this level, each forming two new closely associated groups (Fig. 5*g, h* and *i, j*). This is followed, at a slightly higher level, by a bifurcation of the third phloem group (Fig. 3*f*) to form two separate groups of phloem (Fig. 5*k, l*). All of the six newly formed groups of phloem become further separated by parenchyma at successively higher levels, and three areas (Fig. 7 *h, i, l*) together with one phloem group that does not branch (Fig. 7*c*) become associated with two groups of metaxylem to form two double bundles on either side of the stele (Fig. 7). These double bundles continue at higher levels as midribs of the cotyledons. In the cotyledon one of the remaining phloem strands (Fig. 5*j*) becomes collaterally arranged with xylem by the "migration" of both the xylem and the phloem (Figs. 6–7). This collateral bundle branches into two traces just below the level where the cotyledons separate from the hypocotyl, and each trace becomes a lateral bundle at the margin of each cotyledon (Fig. 8). A second lateral strand to the other margin of each cotyledon is formed at a higher level in the same manner as the first by the "migration" of xylem and a phloem area (Fig. 5*k*) located opposite the first lateral cotyledonary trace (Figs. 6–7). The one remaining unassociated phloem strand (Fig. 6*g*) continues upward in the hypocotyl and becomes continuous with the provascular strand that supplies the epicotyl and the first true leaf.

The conspicuous double arcs of inner cortex accompany each new phloem group in the upper hypocotyl, as was true of the root and the lower hypocotyl. The number of cells in each arc diminishes at higher levels until the usual number in the upper hypocotyl is four. The cytoplasm of



Figs. 1-8. *Echinacea purpurea*

the cells making up the arcs is dense, and these cells become the epithelium of resin ducts that develop schizogenously between the two cell layers. In the lower portion of the cotyledon the large double bundle is accompanied by two resin ducts laterally oriented in reference to the two patches of phloem. At a higher level the double bundles become collateral with the xylem, and the two ducts fuse so that only one duct accompanies the phloem (Fig. 8). Prior to the first branching of the midrib in each cotyledon another duct is formed in close association with the protoxylem. This second resin duct appears to arise from the bundle sheath. Each small lateral strand of the cotyledons has one duct associated with it until it reaches a point just below the place where it branches. At this location another duct appears opposite the first. The venation in the cotyledons corresponds to Lee's "Type 2" classification, in which three vascular strands "enter" the cotyledon, and the first branching in all three strands takes place near the base of the cotyledon.

EXPLANATION OF FIGURES 1–8

Figures 1–8 are camera lucida diagrams of vascular transition in *Echinacea purpurea*. Stippled areas represent phloem; solid areas, xylem

FIG. 1. Diarch root with alternating phloem (*a, b*) and exarch xylem. The double cortical arcs are external to two phloem groups

FIG. 2. Triarch region of lower hypocotyl after the bifurcation of one phloem area (*a*) into two new phloem groups (*c, d*) and the maturation of a third exarch xylem arm. Double cortical arcs are external to three phloem groups

FIG. 3. Tetrarch region of middle part of hypocotyl after a bifurcation of the second phloem area (*b*) into two new phloem groups (*e, f*) and the maturation of a fourth exarch xylem arm. Four cortical arcs are external to the phloem

FIG. 4. Lateral differentiation of the metaxylem in relation to the protoxylem at a level in the upper part of hypocotyl

FIG. 5. Bifurcation of three phloem areas (*d, e, f*) into six new phloem areas (*g, h, i, j, k, l*) and separation of these areas by parenchyma. The fourth phloem area (*c*) does not bifurcate. Resin ducts arise between the double layers of cortex external to the phloem

FIG. 6. Further "migration" of xylem and phloem to form two double bundles on the upper and lower sides and two collateral bundles on the left and right

FIG. 7. A level in the upper part of hypocotyl just before divergence of the cotyledons. The two double bundles continue as midrib bundles of the cotyledons and the two collateral bundles will split to supply each cotyledon with two laterals

FIG. 8. A level above the bases of the cotyledons, showing in each a large collateral midrib bundle derived from the double bundle. Two small laterals are in each cotyledon

The larger branches of the strands do not end blindly in the mesophyll but extend upward in a wavy course and reunite with the larger bundles at a higher level.

Starch grains are abundant in the cotyledons. A nongranular material is also present that stains easily with safranin. Further study should be spent on this species of plant to determine the nature of the inclusions present in the cotyledons.

DISCUSSION

The vascular differentiation in the embryo of *Echinacea purpurea* begins at a level in the base of the cotyledons. As stated earlier in this paper, Phillips (1937) noted that the first vascular tissue of Cynara seedlings matures near the base of the cotyledons and development then proceeds upward and downward. The phloem in the root is defined before the seedling stage is reached. The direction of vascular development of *E. purpurea* is similar to that in Cynara. In both of these species maturation of the xylem and phloem does not occur until after germination. In *Phlox Drummondii* (Miller and Wetmore, 1945), however, potential xylem can be recognized in the procambium of older embryos. The potential phloem arises from the part of the procambium opposite the xylem. By the time the mature seed stage is reached, adaxial procambial cells of the upper cotyledons have become mature protoxylem, and a few abaxial procambial cells in the lower cotyledons show characteristics of immature protophloem. The maturation of xylem and phloem is much earlier, therefore, in Phlox than in *E. purpurea*. A continuous row of mature protoxylem is established in the Phlox seedling that progresses up and down from the point of first maturation near the cotyledonary base. Protophloem cells mature in the same directions as the protoxylem.

The double bundle in the cotyledonary strands of seedlings is a common feature and becomes recognizable at different levels in different species of plants. According to Siler (1931), a double bundle is recognizable at the top of the hypocotyl in *Arctium minus* and extends into the midribs of the cotyledons. A double bundle is present in *Helianthus annuus* at the base of the hypocotyl and continues up into the base of the cotyledons. This study showed that *Echinacea purpurea* is not unlike *Helianthus annuus* in this respect. Several points of difference have been noted in the vascular differentiation of the root and the hypocotyl, however. The root of Helianthus is tetrarch in contrast to the diarch condition found in Echinacea. The triarch arrangement of the xylem in the

lower hypocotyl has not been described for Helianthus. Both are similar in developing six bundles of phloem by meristematic separation of prephloem at a higher level. Two of these areas become collateral with the xylem and provide lateral traces for the midrib of each cotyledon. In Helianthus two lateral traces are differentiated on either side of the double bundle, whereas only one trace is found on each side of the double bundle in *E. purpurea*. In *Arctium minus* the xylem is diarch in the root and in the hypocotyl. Six areas of phloem are delimited that supply the two lateral traces for each cotyledon and the double bundles in the cotyledonary tube. There are three collateral bundles in the cotyledon.

According to Havis (1935), *Tragopogon porrifolius* has a radial diarch root. The transition region is largely tetrarch owing to the formation of two bundles in addition to the two continuous with those of the root. These bundles are formed from metaxylem in the lower transition zone. The cotyledons have a collateral central bundle and two lateral strands; no double bundle is involved.

Thomas (1907) first used the term "double bundle" and reported that some Compositae have an "intermediate type" of venation in the cotyledons. She noted that the slender laterals on each side of the double bundle in the cotyledon fused with the corresponding laterals from the opposite cotyledon and began to form a tetrarch stele in the hypocotyl with the double bundles, but ultimately the laterals died out, so that the root was diarch. The vascular transition from cotyledon to root in *Echinacea purpurea* agrees in most respects with the type observed by Thomas. Hill (1913) added that such a type seemed to be confined to moderately large seedlings. Compton (1912) suggested that "triad" could be used more suitably than "double bundle" because such a bundle more closely resembles a triple bundle than a double one.

Lee (1912) outlined the vascular transition from root to stem in Silphium, Xanthium, Heliopsis, Zinnia, Rudbeckia, Bidens, and other members of the Heliantheae. He concluded that variations occur in even very closely related species, and sometimes in different individuals of the same species, a situation which indicates that "seedling anatomy is of no value in questions of affinity." All specimens that he studied were of the diarch or the tetrarch root type.

The two layers of cells external to the pericycle which are double over the phloem groups have been interpreted as endodermis by Siler for Helianthus. Phillips (1937) described the formation of a double-layered endodermis by a single periclinal division of the inner cortical layer. He

qualified the term "double endodermis," however, by pointing out that Casperian bands appeared only on the innermost cells of this double layer. Oil ducts arise from between the two layers of inner cortical tissue in the manner described for *Echinacea purpurea.* Inasmuch as Casperian bands appear only on the inner layer of cells in *E. purpurea,* the interpretation given in this paper is that the endodermis is one cell in thickness and that the two rows of cells making up the double layer have resulted from an early division of the innermost periblem cells. Williams (1947) has described the root tips of members in the Compositae and suggests that the endodermis functions as a cambium-like tissue that cuts off the linear rows of cortical cells found in many species of Compositae. He also called attention to the prominent intercellular spaces external to the phloem in many species. In Echinacea the cells of the middle and outer cortex are arranged in linear fashion with reference to the double inner layer. The manner in which the inner double layer over each phloem area stands out suggests that these cells become part of a continuous resin duct and that the lumen of this duct stems from the intercellular spaces between the two layers.

SUMMARY

Vascular differentiation begins when the embryo is about 700 microns in length. A dark-stained area extends up into each cotyledon and bounds a lighter staining area just beneath the epicotyl. This is the first indication of a pith.

An embryo of 2.6 mm. length shows a number of strongly developed areas in the procambium throughout the hypocotyl and the cotyledons. These strands later differentiate into phloem. The xylem strands are not delimited at this age. Endodermal cells are enlarged over the developing phloem areas.

The first immature xylem cells are evident in the lower part of the cotyledons in embryos dissected from mature seeds. Maturation of the first phloem element proceeds acropetally and basipetally from the lower levels of the cotyledon.

In twenty-four-hour seedlings the provascular strands of the upper hypocotyl increase in width by longitudinal divisions of the procambium. One or more rows of protoxylem and metaxylem mature into the lower hypocotyl and the upper cotyledons.

Mature phloem elements are first seen in eight-day seedlings.

The root is characterized by diarch, exarch xylem, and a radial ar-

rangement of xylem and phloem. At successively higher levels in the hypocotyl three and four xylem arms are differentiated. The hypocotyl is rootlike throughout the greater length.

At successively higher levels in the upper part of the hypocotyl the metaxylem becomes differentiated laterally in reference to the protoxylem, and bifurcation of three phloem groups provides the upper hypocotyl with seven areas of phloem. Four areas become associated with two laterally differentiated xylem arms and form two double bundles that become the midribs to the cotyledons. Two more phloem areas become collateral with the two remaining xylem arms and branch with the cotyledons to form a lateral bundle at the margins of each cotyledon.

Each strand of phloem in the root and the lower hypocotyl is bounded on the outside by a double arc of cells resulting from an early division of the innermost periblem. In the upper hypocotyl and cotyledons these double cortical arcs become reduced to about four cells, and resin ducts are formed by the schizogenous splitting apart of these cells.

As determined by chromosome counts made from cells of root tips, the diploid number of chromosomes in *Echinacea purpurea* is twenty-two.

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INCREASED MULTIPLICATION AND OTHER EFFECTS OF IRRADIATION ON TULIP BULBS*

TEUNIS VERGEER

TO DETERMINE the effects of slow neutron irradiation on plant materials a lot of 500 tulip bulbs of the early double variety Mr. van der Hoeff was gratuitously contributed by Dr. Willem E. de Mol, of Amsterdam, Netherlands. Of these 470 were irradiated. In nearly all instances the irradiation used permitted a certain amount of development. The plants survived for a variable length of time but eventually all died, leaving no viable offspring (1).

Thirty normal bulbs of the same variety had been packed and shipped in one container with 440 of the irradiated bulbs. The plants which developed from these 30 bulbs showed many marked modifications, which are reported in this paper. Whether these bulbs suffered secondary irradiation from the neutron irradiated bulbs or were irradiated in another manner cannot be positively stated at this time, but subsequent experimentation with gamma rays seems to support the first alternative (see below).

The 30 bulbs were planted outside on December 23. A commercially grown lot of the same variety which had been planted in the same field about 30 feet distant served as controls. Soil conditions, exposure, and fertility were identical so far as could be determined, but the commercially grown lot was planted about November 15. It is common experience among growers that planting at this late date makes very little difference in the time at which the tulips bloom and causes no marked modifications, but tends to reduce the crop.

Some of the experimental tulips developed more slowly than the controls. On the fourth of May, 26 of the 30 plants were above ground. One of these lacked a flower bud, two were only 2.5 cm. high, and 23 were

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10 to 15 cm. high. The flowers of six had developed to such an extent that the yellow color of the petals was pronounced and the diameters of the opening flowers ranged from 2.5 to 5 cm. The commercially grown lot of 150 bulbs, planted 38 days earlier, were about 20 cm. high at this time and had flowers about 10 cm. in diameter. The greatest flower development of the 30 probably was attained by May 12, although the plants were by no means uniform in this or any other respect.

LEAVES

On May 23, when normal plants of this variety were up to 24 cm. high, average 20.9 cm., the height of 24 of our plants ranged from 3 to 24 cm., average 16.38 cm. Except for the smallest plants, no leaf enlargement took place beyond this date. Three plants, nos. 16, 24, and 29, which had previously been used for study, were left or replanted, and three had not come up. One of them, no. 19, had 6.3 cm. of plant development above the bulb. Another, no. 17, had a mass of turgid leaves coiled up in the soil, and the third, no. 15, had two elongated internal buds protruding one fourth and three fourths of an inch above the bulb, which otherwise grew only 4.5 cm. and never reached above the soil. It had no roots and was replaced two inches deep in the soil. The roots of the other two were not investigated, but the 2.5 inches of soil above the underground growth was dug away, and the soil around the leaves was loosened in the hope that the leaves would reach light for photosynthesis. In spite of this, they did not grow above the soil.

Calorimetric methods were not available, but the general impression that the plants which grew to fairly normal size had rather normal chlorophyll development and that the leaves of plant no. 11 were a darker green than those of other tulips should be mentioned.

By May 31 the commercial lot of 150 tulips of the same variety had died down completely. On June 4 the 24 fairly well grown plants of the lot of 30 appeared healthier than ever. All other tulips in the same field, including thousands of Darwins, which normally mature two weeks after Mr. van der Hoeff, had died, with the exception of the variety Carara, which had leaves partly green and partly dried toward the tips. This is known to be a very late variety.

After the Carara and all the other bulbs had been harvested and the field plowed, our lot of Mr. van der Hoeff was still green and aroused much curiosity among growers. Most of them died in the last week of June. In fact, on July 2, when the bulbs were harvested, some of the

plant stems were still partly turgid. However, because of the necessity of making a report, harvesting was undertaken. A similar extension of the growth period was observed by De Mol in irradiated gladioli (2). As was to be expected, the longer photosynthetic period favored crop development (see below).

Modifications were common among the leaves. There were obvious differences in the spacing along the stem. Two plants, nos. 23 and 31, had leaves with the upper ends very blunt, curled, and torn. A dead brown streak was observed in the middle of one leaf of plant no. 20. Several had variegated leaves with reddish or whitish edges. The upper leaves at times were yellow-colored but turgid; at other times, half yellow, half red. One leaf was attached to the stem along one side. Four leaves were split 1.5 to 4 cm. from the apex toward the base. This occurs rarely in normal Mr. van der Hoeff and has been observed in the commercially grown bulbs in 3 per cent of the plants. Any of the variations mentioned may occur in normal plants, but the multitude of variations observed in this small group suggests abnormal influences.

STEMS

Mr. van der Hoeff is a very straight, stiff, and heavy-stemmed tulip, so that it is excellent for formal bedding. Five of the 21 fairly normal plants, however, had obviously crooked stems, most of which bent sharply at the soil-air level. This also appears to be an induced variation.

PISTILS

In 21 plants, pistils and a variable number of abnormally developed petals were observed. On May 21, nine days after most of the flowers had reached a state comparable to full bloom, a dozen or more pistils still appeared to be sufficiently turgid to attempt fertilization, although most of the petals had fallen. Though it is unfortunate that pollination was not carried out earlier, it is possible that seed resulted in three pods. Pistils may remain receptive to pollen as long as ten days after the petals drop, according to Dr. F. W. Went (personal conversation). It is remarkable, however, that enlarging ovules were observed on the outside of some pistils before pollination and on others within two days afterward.

This growth of ovules was not due to fertilization because a period of two days is insufficient for pollen tubes to grow down and insure fertilization. The lack of seed production in the majority of these also indicates that fertilization may not have occurred at all. A hormone response due

to pollination is not excluded as the possible cause of part of this ovule development. The data recorded in the tables show, however, that several pistils had undergone material enlargement before fertilization was attempted. Those which died soon after the petals were only 2 cm. tall, but those which were turgid on or about May 23 were at that time three or more centimeters tall. Formation of ovules on the outside of the ovaries must be attributed to irradiation disturbances.

On May 23 one of these "flowers," no. 23, had only dried parts. Of the remaining 20 flowering plants only four had normal pistils, nos. 3, 9, 13, and 27. They were still growing on June 4. By this time the pistil of no. 27 was 4 cm. tall; the others were somewhat shorter. All eventually dried, and in the capsules of nos. 3 and 27 a few half-sized but otherwise normal-appearing seeds were found. Between May 23 and 27 five pistils were observed to be healthy and growing but modified in various ways. No. 28 was so broadly fasciated at the top that the surface of the stigma measured 3.7 by 1.5 cm. Its length was 3.5 cm. Later it grew an additional 12 mm. in length and developed many healthy red ovules on the lateral surfaces and finally some small seeds.

On May 23 no. 2 had a split from which 16 enlarged healthy ovules protruded to the outside. The split continued to become deeper, and 12 days later more healthy ovules had become visible, but no seeds resulted. The pistil of no. 31 also developed many external ovules which noticeably enlarged, but the enlargement was unilateral. It caused the ovary to become much distorted, and eventually the part with the ovules broke loose. No seeds resulted. Marked splitting of the upper part of the pistil occurred in no. 30, but little further development took place.

On May 23 the pistil of no. 18 had the upper 7 mm. markedly swollen. The stigma was purplish blue, whereas light green is normal. The pistil of no. 25 appeared to be growing on one side but drying on the other. On no. 26 only the stigma was drying, and on no. 20 the stigma was dried out but the ovary was turgid. The pistil of plant no. 7 also appeared normal in shape, but its color was much lighter green than usual. The pistil of no. 10 was losing its color; the pistils of plants nos. 5, 6, and 11 were drying. Three other pistils, on plants nos. 12, 21, and 22, were dried out by this time.

It should be emphasized that none of the pistils of the 150 commercially grown plants showed any enlargement, in spite of the fact that all flowers were left to dry naturally. The staminoid petals of this variety are known to be sterile, so that self-fertilization is impossible. Many

other early tulips in the field were blooming at the same time as the commercially grown control lot. Therefore cross-fertilization was possible, but none of the 150 produced any seed. Since 10 of the 20 pistils of the experimental plants lived longer than usual and enlarged markedly while only three developed any seeds, and those abnormally small in size as well as in quantity, the author interprets the unusual development in the seven which produced no seeds as parthenocarpy, probably due to irradiation. Enlargement due to pollination effects should also be considered as a possible explanation.

Though fertilization is most likely the cause of seed production in the three experimental pods, the slight amount of seeds and the obviously unusually small size raise the question whether they could be haploid. All seeds have been sown. If they grow, we might get plants with 12 chromosomes instead of 24, which is the known number of Mr. van der Hoeff, according to Dr. W. E. de Mol (personal communication). The univalent condition may also reveal unknown recessive characteristics and may provide a clue to the original species from which Mr. van der Hoeff and related tulips have been derived. Since some seeds formed in three pods, we assume that all other ovaries which enlarged were completely sterilized by the secondary irradiation.

PETALS

In general, petal development was also decidedly abnormal. The normal petal color of this variety is almost uniform light yellow, subject to fading to white. Plant no. 7 had some petals with considerable reddish-brown pigment at the upper edges and others in which this pigment extended halfway down the petals. No. 9 still had turgid outer petals on May 24. They were greenish except for a brown central patch and whitish edges, often lined with a fine brown feathered stitching. The inner petals (staminoid) had all the distal halves dried, but the proximal halves were still turgid. In no. 12 a few outside petals also were still turgid on May 24. They were predominantly yellow on the inside with white edges, but green on the outside. The petals of no. 13 were similar, but had brownish edges instead of white. The inner petals seemed badly scorched; the outside ones were turgid.

ASEXUAL REPRODUCTION

The most remarkable phenomenon displayed by these tulips deals with vegetative reproduction. Unfortunately, no exact records on the

normal rate could be obtained from the commercial growers, though all agree that it is very low as compared with those of other tulip varieties. Schoonoord, a sport of Murillo, from which Mr. van der Hoeff is derived, is also an early double variety. Full-sized bulbs of this kind had been planted on the show grounds of a grower and were harvested but not cleaned. Of these I made a random selection of 40 bulbs which evidently had not lost any offsets. The total harvest of these 40 bulbs consisted of 21 large bulbs (11–12 cm. in circumference), 18 smaller blooming-size bulbs, and 42 ranging below this size to very small. It was interesting to note that 14 had merely replaced themselves, 14 produced two bulbs, nine each three bulbs, and three four bulbs each. The average rate of bulb production, counting all sizes, was slightly over two. This is typical of the early double tulips not only in Michigan, but also under the cultural conditions obtaining in the Netherlands.

In comparison with these figures 21 undisturbed plants which produced some kind of flower averaged 8.14 bulbs and bulblets per plant; the minimum was four, and the maximum, eleven. The total weight of the new bulbs produced by these plants ranged from 21.2 to 48.5 grams, average 35.46 grams. The average weight of 37 normal maximum-size bulbs of Mr. van der Hoeff is 20.4 grams. Our data indicate that parthenocarpy does not interfere with crop production, possibly because of extensive photosynthesis by the carpels. It is generally held that seed production does reduce the bulb crop. Since only three plants yielded seeds, our data are inadequate to justify conclusions on this point.

It is remarkable that plant no. 15 had four bulblets, weighing a total of 7.8 grams in spite of the fact that it never formed roots or developed any leaves. No. 17 grew leaves in the soil, but they never came up. It developed seven bulblets with a total weight of 15 grams. Similarly, no. 19 produced three bulblets, weighing a total of 12.3 grams.

In addition to the accelerated rate of reproduction, departures of the new bulbs from the parent characteristics were also observed. Clone 5 had a markedly rougher and whiter tunic. Clone 30 was so oddly rounded that the bulbs resembled small potatoes, and it was almost impossible to tell the apex from the root crown. Three (nos. 9, 18, and 31) produced one bulb each in the axil of a leaf underground. The last variation also occurs occasionally in normal bulbs. For the convenience of the reader most of the results described are combined in Tables I–IV.

In retrospect it is very clear that an unusual influence has caused many changes which can hardly be explained except on the basis of secondary irradiation from radioactive materials. It must also be remem-

bered that all plants underwent what probably is a temporary stunting effect. This normally disappears after the second crop, at least when X-ray is used (3).

GAMMA EXPERIMENT

If the irradiation of these tulips was due to radioactive chemicals[1] in the bulbs with which they were packed, the influence of beta rays was probably negligible and gamma rays must have been largely responsible. To test this hypothesis a gamma irradiation experiment with the same variety of tulips is now in progress. Twenty bulbs were retained for controls. Forty were exposed to Co^{60}, which emitted 10 mc. from a glass vial placed in the center of the tulip bulbs for 28 days.[2] The nearest tulip bulbs had their centers 1 cm. from the source. In air the available energy at this point was $mr/hr \frac{5.6 \quad .01 \quad 2.4 \quad 10^6}{1} = 134.4\ r/hr$ or $28 \times 24 \times 134.4\ r = 89316.8\ r$ in all. The greatest distance between the source and the center of the bulbs in the periphery was 10 cm. The absorption by the tulip tissues is unknown, but it is probably very high, and it affords considerable protection for all but the nearest tulips.

The glass of the vial probably screened out all beta rays. If it actually did so, the energy emitted should represent pure gamma rays.

The wide variation in the present experiment should be a good approximation of what happened to the lot discussed in this paper. The distance from their source of irradiation must also have varied considerably. Thirty days after exposure all 37 available gamma-irradiated tulips had failed to develop a visible apical bud. Every one of the 20 controls from the same original lot, kept under nearly identical conditions, had made a visible apical growth from a few millimeters to more than one centimeter. Root-crown development was also markedly delayed in the irradiated lot, but much-enlarged root crowns with many individual root tips were the rule in the 20 controls. Since inhibition of growth and root development was characteristic of irradiation effects in the first set of experiments, the author is encouraged to believe that gamma rays were also responsible for the effects on the 30 tulips reported in this paper.[3]

[1] Primarily sodium (personal conversation with Dr. Norbert J. Scully, of the Argonne National Laboratory).

[2] Courtesy of Dr. Lester Wolterink, Michigan State College.

[3] By July 15, 1950, reduction in the height of the plants, marked development of lateral buds, increased rate of multiplication, increased crop production, and marked parthenocarpy had resulted from the gamma radiation.

SUMMARY

Thirty tulip bulbs which were packed and shipped with 440 neutron-irradiated bulbs afterward underwent marked physiological and morphological modifications. A commercial lot of the same variety, grown 30 feet distant in the same field, under practically identical conditions, was used as controls.

Three tulips failed to come up; three others were used for study. Twenty-four grew 3 to 24 cm. high, average 16.38 cm. Normal plants did not exceed this maximum height, but averaged 20.9 cm. The experimental plants lived about one month longer than the controls. The following departures from normal were observed in their leaves: modified spacing along the stems; failure in development of the distal ends, causing them to be much curled and torn; variegated coloring; upper leaves partly or wholly petal color; splitting of the apices of the leaves for a variable distance; and, in one leaf, a dead brown streak.

Twenty-one plants developed flowers, but all were abnormal. Many petals were badly burned and failed to develop. Instead of the almost uniform yellow color, many were variously marked with red, brown, white, and green, or with a combination of these colors.

Most of the pistils were split, fasciated, bent, or otherwise abnormal. In some, pigmentation was lighter than usual, others were reddish, one had a purplish-blue stigma. In still others the stigma appeared burned. Ten of twenty pistils lived much longer than those of the controls and enlarged markedly. Seven of these produced no seed. The enlargement probably is parthenocarpy due to irradiation effect, but it may be due to pollination of sterilized ovaries. Three plants developed some small seeds, but mostly hulls. Self-fertilization is excluded. Three pistils, including two of the three which produced seeds, developed enlarging ovules on the outside, which colored red.

Forty closely related early double tulips under somewhat more favorable conditions produced a total of 81 bulbs or bulblets, an average of 2.02 bulbs per plant. Twenty-one undisturbed experimental plants each produced four to eleven bulbs or bulblets, an average of 8.14 per plant. The longer photosynthetic period is probably an important contributory factor. Ovarian growth did not appear to interfere with crop production. Bulbs which did not grow, or which developed only underground growth, produced three to seven bulblets. Departure from the normal shape of the bulbs, as well as differences in color and texture of the tunics, occurred.

Since irradiated tulips are most likely to affect others by the gamma

rays which they produce, a control experiment with gamma rays was undertaken. Thus far the same delay in development has been observed as in the recorded experiment, which supports the hypothesis that the effects reported are due to secondary gamma irradiation.

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TABLE I

CULTURAL DATA ON FIVE PLANTS WHICH PRODUCED EXTERNAL OVULES OR SEED

Date of observation, 1949	Place number	Height to pistil tip, cm.	Highest leaves, cm.	Number of leaves above ground	Other modifications	Petals	Pistil on date in Column I	Pistil later	Bulb and bulblets harvested 7/6/49 *	Total weight of crop 7/9/49
5/23	2	23	19	5	Leaf 4.5 cm. below ovary, half yellow, like flowers	Yellow and crinkled; had dropped 5/23	Healthy, split on one side; 16 ovules growing to outside of split	6/4: Split deeper; more ovules on outside 6/15: Dried out	11	45
5/27	31	21.5	17	4	Two leaves much split and curled; similar to 23	Dropped	3.5 cm. dark green, bent. Good enlarged ovules on one side; many small ones lower down	6/4: More bent. Swollen on one side. Part with ovules breaking loose	8	37.5
5/27	27	24	16.5	4	Stem not quite straight	Dropped	3.5 cm., 1.8 cm. wide at top; healthy in appearance	6/4: 4 cm. swollen 7/2: Some seed	10	30.7
5/27	28	23	19.5	6	Two upper leaves largely yellow-colored and turgid	Dropped	3.5 cm., broadly fasciated. Stigma 3.7 x 1.5 cm. Healthy, red ovules on both sides	6/4: 4 cm. More ovules showing, much enlarged 7/2: Some seed	7	37
5/23	3	22.7	18	4	.....	Dropped	Normal	6/4: 5 cm. swollen 7/2: Some seed	7†	21.2

* One bulblet of 5 grams found loose, cannot be identified. † Oddly formed.

TABLE II

CULTURAL DATA ON TEN PLANTS OF WHICH THE OVARIES ENLARGED WITHOUT SEED PRODUCTION

Date of observation, 1949	Place number	Height to pistil tip, cm.	Highest leaves, cm.	Number of leaves above ground	Other modifications	Petals	Pistil on date in Column I	Pistil later	Bulb and bulblets harvested 7/6/49	Total weight of crop 7/9/49
5/24	13	20	19	4	.....	All present. Inner ones scorched. Outer ones turgid, varied colors	Normal	6/4: 3.5 cm., turgid; later dried; no seed	9	44.5
5/24	9	19	19	5	Stem slightly crooked	Mostly present, half dried. Outer green and varied colors	3.5 cm., normal	6/4: Dried	9 *	36.2
5/24	10	21	18.5	4	.....	Dropped	3.5 cm., normal, losing color	6/4: Dried	6	36.3
5/27	30	23	19.5	5	Stem almost erect	Dropped	3.4 cm., green except upper part seems scorched and cleft several times	6/4: Dried	8	37.5
5/27	25	20.5	18	3	Third leaf 5 cm. below pistil has edges reddish and white	Dropped	3.5 cm., normal, growing on one side, drying on the other	6/4: Dried	7	36.3

TABLE II (*Continued*)

CULTURAL DATA ON TEN PLANTS OF WHICH THE OVARIES ENLARGED WITHOUT SEED PRODUCTION

Date of observation, 1949	Place number	Height to pistil tip, cm.	Highest leaves, cm.	Number of leaves above ground	Other modifications	Petals	Pistil on date in Column I	Pistil later	Bulb and bublets harvested 7/6/49	Total weight of crop 7/6/49
5/23	7	20	19.5	6	One inch stem between each two leaves	Mostly turgid except few central ones to one side. Reddish-brown markings	Light green, turgid	6/4: Dried	9	34.8
5/27	18	21.5	20.5	5	.....	Dropped	3 cm., upper 7 mm. swollen, purplish blue	6/4: Dried	9 *	48.5
5/27	20	19.5	19	5	Stem crooked. One leaf with dead brown streak through center. Leaf half yellow and half red	Dropped	Reddish, narrow, spreading; stigma dried out	6/4: Dried	9	39.5
5/24	11	22.5	17.5	3	Basal leaf very wavy at edge. Plant at 80° angle. Leaves darker green than those of other tulips	Dropped	Normal, 3 cm. drying	6/4: Dried	4	34.9
5/27	26	20	15	4	.....	Dropped	3 cm., drying stigma, deeply divided	6/4: Dried	9	31.5

* One bulb one inch above the others.

TABLE III

CULTURAL DATA ON SIX PLANTS OF WHICH THE PISTILS WITHERED WITH THE FLOWERS

Date of observation, 1949	Place number	Height to pistil tip, cm.	Highest leaves, cm.	Number of leaves above ground	Other modifications	Petals	Pistil on date in Column I	Bulb and bulblets harvested 7/6/49	Total weight of crop 7/9/49
5/27	21	15.5	17	3	Stem crooked	Poor; distal parts dried	2 cm. long, dried	9	25.5
5/27	22	14.5	14	6	Upper leaf fused in part with stem. One inch edge white and pink	All dried. One petal 8 mm. below flower	2 cm., dried	8	26.3
5/24	12	19	20.5	4	.....	One quarter present. Varied colors	Dried out	9	47.7
5/27	23	11.5	11	4	All upper edges much curled and torn in appearance	Dried flower bud	Dried flower bud	6	38.5
5/23	5	18	17	6	.....	One left	Dying, split two fifths of length	7 *	29.3
5/23	6	18	17	6	Grows at angle of 15° from vertical. One split leaf	One greenish. Several dried	Dying	10 †	26

* Whiter, rougher tunic. † One bulb one inch above the others.

TABLE IV

CULTURAL DATA ON NINE PLANTS WHICH DID NOT BLOOM, DID NOT COME UP, OR WERE DISTURBED DURING THE GROWING PERIOD

Date of observation, 1949	Place number	Highest leaves, cm.	Number of leaves above ground	Remarks	Bulb and bulblets harvested 7/6/49	Total weight of crop 7/9/49
5/23	4	5.5	2	Roots not investigated	1	5.8
5/24	14	3	2	Roots not investigated	5	23
5/27	17	0	0	Turgid leaves curled in soil. Tip of internal bud showing above bulb. Dug away 2½″ of soil to give it a chance	7	15
5/27	19	0	0	2½″ growth above bulb. Dug away 2″ of soil to give it a chance	3	12.3
5/25	15	0	0	Shoot 1¾″, two internal buds ¾″ and ¼″ above bulb. No roots. Replaced 2″ deep	4*	7.8
5/27	24	0	0	Internal bud 2 cm. above bulb. Stem and leaves used for study. Covered and left; roots not investigated	8	17.7
5/27	29	0	0	Stem broken off; internal bud ¼″ above bulb. Replanted after earlier inspection. Bulb 3″ deep	5	11.5
5/24	16	12.5	4	Dried up. Was dug up for root collection May 20	6	18.5
5/27	32	0	0	Dried up, used before for roots	6	22.4

* One of the four was partly eaten.

FORESTRY

SOME RESUPINATE POLYPORES FROM THE REGION OF THE GREAT LAKES. XXII*

DOW V. BAXTER

THIS series of papers (2) is offered as a conservative summary of our knowledge of the taxonomy of the resupinate polypores of North America, their occurrence and natural and artificial ranges, the hosts and the substrata attacked, their reaction in culture, and their importance. In this collection of widely distributed species that belong to several genera a large amount of variation is to be expected. Several plants described become resupinate only under certain conditions, but these species are included, in this series, not only because of the taxonomic problems they create, but also because of the possible economic significance of some of them when growing in artificially created environments.

This paper emphasizes certain unusual environments, host, and substrata for some of the common members of the group and presents descriptions of *Lenzites saepiaria* and *Polyporus licnoides*.

The color terms given within quotation marks are those of R. Ridgway, *Color Standards and Color Nomenclature* (Washington, 1912).

Polyporus licnoides Mont., Pl. Cell. Cuba 401. 1842

Polystictus licnoides Fr., Nov. Symb., 92. 1851.
Polystictus subglaber Ellis and Macbr., Bull. Lab. Nat. Hist. Univ. Iowa, 3: 192. 1896.

*Throughout the work on these monographs (2) I have been indebted to many individuals and institutions for suggestions, help, and privileges extended to me. Grants from the Horace H. Rackham School of Graduate Studies of the University of Michigan have greatly facilitated both the field and the laboratory studies. My appreciation is expressed particularly to the men who have accompanied me on my numerous expeditions to Alaska, the Yukon Territory, the Northwest Territories, Newfoundland, and Labrador. Much credit is due them for aiding in the collection and care of specimens and for living, at times, under rather difficult circumstances. I am under obligation to Professor T. G. Halle, of Naturhistoriska Riksmuséet in Stockholm, with whom I have had the pleasure of association. Thanks are also due to several American institutions and scholars. To the authorities at the New York Botanical Garden, to the staff of the Division of Pathological and Mycological Collections of the United States Department of Agriculture, and to the Division of Botany, Central Experimental Farms, Ottawa, Canada, I am especially indebted.

Hapalopilus licnoides (Mont.) Murr., Bull. Torrey Bot. Club, 31: 417. 1904.
Polyporus subtropicalis Spegazzini ex Lloyd (*The Genus Polyporus*, p. 387. 1915); *Polyporus xerophyllaceus* Berk., Hook. Journ. Bot., 8: 200. 1856; ex Romell in Murr., Bull. Torrey Bot. Club, 31: 417. 1904.

Fructification on wood of southern hardwood trees, thin, coriaceous, imbricate, aplanate, or sometimes resupinate; surface multizonate, concentrically striate, finely tomentose to subglabrous, subshining, brown with buff zones, "tawny olive," "cinnamon," "army brown" to "bister," and typically with smooth brownish-red areas on the pileus; context thin (1 mm.); tubes short, 1–2 mm.; spores ellipsoid or subglobose, hyaline 3–4 × 2–3 (Murr.); setae brown.

Allied species.—This plant, common in subtropical parts of Florida and elsewhere in America, is closely allied to *Polyporus gilvus*. It may with reason be considered a thin form of *Pol. gilvus*, but the name has become so well established that it seems best to retain it. Although certain growth forms of *Pol. licnoides* and *Pol. gilvus* appear to be nearly alike, the two plants are ordinarily distinguished by the numerous concentric zones which ornament the surface of *Pol. licnoides*. The context is usually rigid in *Pol. gilvus*, whereas that of *Pol. licnoides* is ordinarily more flexible (17). In typical specimens of *Pol. licnoides* smooth reddish areas occur on the fructification to a greater extent than in most specimens of *Pol. gilvus*. The pileus in *Pol. licnoides* is much more zonate.

Because of some similarity in their specific epithets *Polyporus lignosus* Klotzsch might be confused with *Pol. licnoides*, but its color and its conspicuously multizonate pileus differentiate it from *Pol. gilvus*.

Since *Poria rufitincta* Cooke sensu Murrill is both thin and ferruginous and assumes a brown-reddish tinge, it might be mistaken for a resupinate specimen of *Polyporus licnoides*. Furthermore, the mouths of both plants are small, i.e. mostly seven to a mm., and both have setae. However, the spores are ellipsoid to subglobose and measure 3–4 × 2–3 μ (Murrill) in *Pol. licnoides* and are subglobose and larger and measure 4–5 μ in *P. rufitincta*. *Pol. licnoides* early exhibits a reflexed habit of growth, so that care should be taken in the field to collect material which shows this tendency. *P. rufitincta* cracks somewhat upon drying, a feature which is only relative, but one not so likely to occur in *Pol. licnoides*.

Polyporus extensus is another tropical plant which might be confused with *Pol. licnoides*, but it usually has stratified tube layers and is ordinarily a thicker plant than *Pol. licnoides*. The spores of *Pol.*

extensus are described as fulvous, whereas those of *Pol. licnoides* are hyaline.

Fomes conchatus, in a resupinate state, may also bear some resemblance to *Polyporus licnoides,* but it, too, is a much thicker plant and ordinarily exhibits the stratified tube layers. The plant determined as *F. Ribis,* a very close relative of *F. conchatus,* has been confused with *Pol. licnoides.* Setae are abundant in *Pol. licnoides,* whereas *F. Ribis* has no setae.

Habitat.—*Laurocerasus caroliniana, Liquidambar Styraciflua, Magnolia grandiflora, Melia azedarach, Myrica cerifera, Persea Borbonia, P. palustris, Prosopis juliflora, Quercus Michauxii, Q. virginiana, Sapindus marginata, Sassafras sp., Torreya taxifolia.*

Distribution.—Florida, Louisiana, Mississippi, Missouri, South Carolina, Tennessee, Texas.

Occurrence.—*Polyporus licnoides* occurs in North America most generally in the southern United States, but elsewhere it appears more widely; in semitropical and tropical areas. It is known from Argentina, Brazil, British Guiana, British Honduras, Colombia, Costa Rica, Cuba, Dutch East Indies, Guatemala, Haiti, Jamaica, Mexico, New South Wales, Nicaragua, Panama, Peru, Philippine Islands, Venezuela, and Virgin Islands.

Lenzites saepiaria (Wulf.) Fr., Ep. 407. 1838

Agaricus hirsutus Schaeffer, Fung. Bavar., 4: 33, pl. 76. 1762. Teste Murrill, 1908.
Agaricus saepiarius Wulfen in Jacq. Coll., 1: 347. 1786.
Agaricus boletiformis Sowerby, Engl. Fungi, pl. 418. 1814. Teste Murrill, 1908.
Daedalea saepiaria (Wulf.) Fr., Syst. Myc., 1: 333. 1821. Fries, Obs. Myc., 1–105. 1815. Teste Murrill, 1908.
Gloeophyllum saepiariarium (Wulf.) Karst., Karsten, Hattsv., 2: 80. 1882.
Gloeophyllum hirsutum (Schaeff.) Murr., Journ. Myc., 9: 94. 1903.
Gloeophyllum abietinellum Murrill, North Am. Fl., 9: 129. 1908.
Lenzites rhabarbarina Berkeley et Curtis, Ann. Mag. Nat. Hist., II, 12: 428. 1858. Teste Murrill, 1908.
Lenzites sepiaria porosa Pk. ex Lowe, Pol. New York, 108. 1927.
Sesia hirsuta (Schaeff.) Murr., Journ. Mycol., 9: 88. 1903.

Fructification coriaceous, sessile, dimidiate, effused-reflexed or sometimes resupinate; 1–4 × 9–10 × 0.5–1 cm., surface "argus brown," "bone brown," grayish black on weathering, surface anoderm, tomentose, or strigose, smooth or slightly tubercular, zonate, margin rather thick, nearly entire; context soft, punky, homogenous, yellowish brown, "ochraceous tawny" or "argus brown" in old plants, 1–3 mm. thick; usually lamellate below, anastomosing at first, "light ochraceous buff"

to "ochraceous orange" or grayish, in poroid forms tubes circular, 1–2, mostly 2, to a mm., edges thick, entire; basidia 4.5–6 × 18–30 μ (Pilát); spores hyaline, cylindrical, 3–4.5 × 7–12 μ,[1] without conspicuous cystidia, sometimes with cystidioles (hypha-like with encrusted ends) 4–6 μ in diameter.

Allied species.—A closely related polypore to *Lenzites saepiaria* is *Trametes odorata* (Wulf.) Fr. Emphasis was once given to the suggestion that they were identical because of the occasional occurrence of the two growing near together or even on the same piece of wood. Furthermore, the hymenium of *Lenzites saepiaria* is often so variable that there is reason for confusing the species (Pl. I). It may be lamellate, daedaloid, or somewhat poroid or irpiciform if growing on unusually wet wood (25).

The difference in the temperature reactions of the two organisms in culture supports the now accepted view that *Trametes odorata* is a species distinct from *Lenzites saepiaria.* A test of growth upon a single agar at temperatures from 30° to 36° C. would serve to distinguish the fungi in culture.

In tests made on cultures of the two fungi (26) there is no apparent difference in the optima of the two species. *Trametes odorata,* like *Lenzites saepiaria,* has an optimum temperature—between 30° and 34° C. Their upper limits of growth are, however, different. *L. saepiaria* is not inhibited until after 40° C. is reached, whereas *T. odorata* was only barely growing at 38° C. and would not develop at all at 40° C. Furthermore, the rates of growth of the two organisms differ. *L. saepiaria* grows faster at all temperatures, the rate being more pronounced between 28° and 30° C.

Their odors may usually be used to separate *Lenzites saepiaria* in cultures from the related *Trametes odorata,* which has a distinct aromatic odor like fennel, whereas *L. saepiaria* does not usually have an odor.

Among the noteworthy microscopic features of the mycelium "medallions" should be mentioned. Apparently they are observed only on wood and not in artificial culture.

The European *Lenzites abietina* is closely related, but Shope (23)

[1] Snell (25) reports that spores from fruiting bodies that appear on roof timbers inside cotton mills are "often smaller than those from fruit bodies collected out of doors. They have been found to measure 6–9 × 2.5–3 μ (mostly 6–7 × 3 μ), whereas 8–12 × 2.5–4 μ are reported measurements given by most mycologists."

separates these two fungi on the basis of the presence of ventricose cystidia in the latter.

Habitat.—Abies amabilis, A. balsamea, A. concolor, A. Fraseri, A. grandis, A. lasiocarpa, A. magnifica shastensis, Acer pennsylvanicum, A. rubrum, Alnus tenuifolia, Arbutus Menziesii, Betula lutea, B. papyrifera, B. papyrifera occidentalis, Chamaecyparis nootkatensis, C. thyoides, Cupressus guadaloupensis, C. macrocarpa, Fraxinus americana, Juniperus pachyphloea, Larix europea, L. laricina, L. leptolepis, L. occidentalis, Picea Engelmannii, P. excelsa, P. glauca, P. mariana, P. pungens, P. rubra, P. sitchensis, Pinus Banksiana, P. contorta, P. echinata, P. glabra, P. Lambertiana, P. laricio (Corsican), *P. monticola, P. Murrayana, P. palustris, P. ponderosa, P. resinosa, P. rigida, P. Strobus, P. sylvestris, P. taeda, P. virginiana, Populus tremuloides, Prunus pennsylvanica, Pseudotsuga taxifolia, Salix discolor, Sequoia sempervirens, Taxodium distichum, Thuja occidentalis, T. plicata, Tsuga canadensis, T. heterophylla, T. Mertensiana.*

Distribution.—Alaska, Northwest Territories, Yukon Territory; Alberta, British Columbia, Labrador, Manitoba, New Brunswick, Newfoundland, Nova Scotia, Ontario, Prince Edward Island, Quebec, Saskatchewan; Alabama, Arizona, Arkansas, California, Colorado, Connecticut, Delaware, District of Columbia, Florida, Georgia, Idaho, Illinois, Indiana, Iowa, Kansas, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Montana, Nebraska, New Hampshire, New Jersey, New Mexico, New York, North Carolina, North Dakota, Ohio, Oregon, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, Texas, Vermont, Virginia, Washington, West Virginia, Wisconsin, Wyoming.

Occurrence.—Lenzites saepiaria, one of the most abundant fungi on dead coniferous timber in North America, is worldwide in its distribution. It is not nearly so common a cause of decay of softwood in Great Britain as on the continent of Europe and in North America (9).

The fungus causes extensive damage by its occurrence on exposed timber in service, especially poles, posts, and ties. It is known on hardwoods (Pl. II), but it is a much more common destroyer of coniferous slash. Wet environments and long exposure in such places are particularly important factors influencing the abundance of the fungus. For example, after a storm of extraordinary violence in the Olympic Peninsula, Washington, *Lenzites saepiaria* occurred abundantly on western hemlock, *Tsuga heterophylla,* a species that con-

stitutes a large part of the volume of overmature West Coast timber. It appeared sparingly, however, on silver fir, *Abies amabilis*, and no decay was attributed to the fungus in western red cedar, *Thuja plicata*. The small amount of rot attributed to this fungus in other timbers was slight in comparison with that caused by *Ganoderma* (*Fomes*) *applanatum* and *Fomes pinicola* (5). All the woods are given in this series or substrata for *L. saepiaria*. On the other hand, fruiting bodies may develop under favorable conditions and have been known to form in green timber within five months (5). In general, its occurrence in standing living timber has been either overlooked or reported as rare (4).

Its significance as a possible agent of destruction of living trees has been underestimated, chiefly because there are few environments that promote its occurrence in standing timber.

Forest practices in the plantations of jack pine, *Pinus divaricata*, on the Nebraska National Forest have resulted in conditions that favor development of *Lenzites saepiaria* (Pl. III). Severe sunscald injury has resulted because of pruning (see section "Decay in Living Trees").

Cultures.—Isolated from *Picea mariana*, Ann Arbor, Michigan; from *Picea mariana*, Goose Bay, Labrador; Central Experimental Farm 17246); from *Betula alba papyrifera*, Goose Bay, Labrador; Central Experimental Farm, Ottawa (17240).

Lenzites saepiaria exhibits so much variability even within the same isolate that variability appears to be a feature that must be considered in the diagnoses of cultures. Cultures often show a mat ranging from a white more or less even-granular or powdery surface to one that is irregularly tufted with thick cushions of brown cottony mycelium. Most cultures develop this tufted growth in age. Snell (23) points out that cultures can be readily distinguished by the scant superficial mycelium and by the powdery appearance given by the oidia. In seven days a mat with a radius of 20 mm. is produced. In fourteen days a mat with a radius of 41 mm. or more develops; it is velvety, "ochraceous orange," "raw sienna," or "amber brown" and has "maize yellow" margins.

The allied *Lenzites trabea* exhibits a paler brown ("orange buff" or "ochraceous salmon") mycelium than that produced by *Lenzites saepiaria*.

Fructification in culture.—Two general types of fructification may

form in malt-extract cultures: (*a*) basidia, which may grow directly on the mycelium, and (*b*), after a minimum of about three weeks' growth, white cushions, which are composed of aerial mycelium. Some of these formations may appear slightly stipitate. They gradually change color, passing through various shades of yellow and finally are "cinnamon" to "Prout's brown." This form of fructification is said by Cartwright (7) to suggest the general form of a Sparassis, with bifurcating tips, but the tips may be branched or unbranched. Individual segments may be flattened, although not to such an extent as to approach lamellae in appearance.

In the less specialized type of fructification slightly raised cushions may appear scattered over the surface of the culture, or they may be widely effused and scarcely raised above the level of the surrounding mycelium. These cushions are "capucine yellow," "cinnamon rufous," "russet brown," or "mikado brown." The hymenial layer occurs over the surface, and basidia often appear directly on the mycelium, apparently with no specialized hymenial layer, as in the genus *Hypochnus*.

The basidiospores produced are viable. Cartwright (7) finds they are usually shorter than those borne on normal fruit bodies, but are otherwise similar. The spores are cylindrical and curved, and measure 6–8 × 3–3.5 μ Secondary spores may also develop in culture. Chlamydospores are formed on the submerged mycelium, and on the aerial mycelium pear-shaped oidia develop.

Cultures of *Lenzites saepiaria* resembling somewhat those of *Trametes odorata* often produce a mat of sodden appearance with no trace of aerial growth. When aerial growth does develop, it is mostly as secondary mycelium. This is characterized by the rich production of oidia, which lend to it a more or less powdery appearance (24).

The tertiary mycelium, which in color and texture resembles the tramal tissues of the sporophores, is often arranged in radiating rows, frequently merging together to form longer ridges, or wider cushions, or mats (24, 18).

Cultures usually stain the agar dark red brown, though not always. The agar stain seems, however, to be the only character which is approximately constant within the same isolation (22).

Fructifications (isolate from *Picea mariana,* Labrador) have appeared in the Michigan wood-block cultures of both red gum (*Liqui-*

dambar Styraciflua) and white pine (*Pinus Strobus*) in one-year-old tests. These appear much like a minute Sparassis as described by Cartwright and Findlay (8). No fructifications have appeared on either red-gum or white-pine blocks in two-year-old tests made with the isolate from birch.

The highest growth rates have been observed by Robak (22) on malt and potato-dextrose agars, and the rate was decidedly slower on xylose than on the other sugars tested. Development on media containing nitrogen of different types is variable, except that the growth is slow on NH_4NO_3 and $(NH_4)_2SO_4$.

The temperature for optimum growth of *Lenzites saepiaria* on a number of isolates has been tested by different investigators. Snell and his collaborators (26) note that the optimal range of the isolates they used was between 30° and 34° C., the best growth occurring perhaps at 32° C. Humphrey and Siggers (13) obtained satisfactory growth from 30° to 36° C.; the highest growth rate was at 36° C. (These authors used a medium which contained beef extract in addition to malt.) Robak (22) found that in five Norwegian and two Canadian isolates the best growth was obtained at 32° C., and that at 30° C. the development was only slightly slower, results which conform well with the observations made by Snell and his collaborators. At 35° C. growth was retarded, and it was checked at 38° C. in four isolates, including the two from Canada. Snell, Hutchinson, and Newton (26) observed a growth at 38° C., which was about half as rapid as the optimal one, whereas at 40° C. the growth rate appeared to be about the same as that observed at 38° C. Growth was not stopped until a temperature of 43° C was reached. Robak (22) calls attention to the fact that the diverging results should be interpreted as due to differences in temperature resistance within the individual strains. The two Canadian cultures of the isolates he tested belong to the least resistant strains.

Snell (25) found that an exposure of three and one-half days to 44° C. or of twelve hours to 55° C. under moist conditions was necessary to kill *Lenzites saepiaria* growing on small blocks of Sitka spruce, whereas with dry heat the temperatures necessary to kill in three days were from 70° to 90° C.

Microscopical appearance in culture.—The submerged hyphae are colorless, thin-walled, abundantly septated, seldom branched, and almost always without clamp connections; they measure 1.5–5.1 μ, being

mostly about 3 μ in width. Oidia or chlamydospores sometimes present. Aerial mycelium colorless, branched, soon breaking up into oidia. Clamps sometimes present. Oidia colorless, mostly ellipsoid, ovoid to globose or pyriform, more rarely cylindrical, measuring 4–35 × 2.5–3 μ (22, 24).

The tertiary mycelium between each two septa is long, stiff, sparingly branched and septate, most often with a clamp connection, more or less approaching the medallion type found in decayed wood (22).

Robak (21) reports that on gallic-acid media there was seldom any oxidase reaction and that it was often late in occurring. Sometimes it was weak, and only rarely was it very strong. There was no reaction on tannic acid. No discoloration of aniline blue was noticed by Robak.

Spore germination.—Basidiospores germinate readily in one or two days in nutrient agar and even in tap water. Snell (24) reports that diffuse light had no effect upon germination, but most of the spores were killed upon exposure to direct sunlight for three days. He states that basidiospores do retain their viability under dry conditions for long periods; 25 per cent germinated after storage for two years and ten months.

Decay in culture.—Robak (21) found that *Lenzites saepiaria,* when cultivated on chip material and blocks of pine and spruce, sap and heartwood, and on sawdust of spruce sapwood, causes reductions in dry weight approximating that produced by *Trametes serialis* and *T. odorata* (22). According to expectation, large losses in cellulose were caused by this brown rot fungus. However, considerable decomposition of the lignin also took place in advanced stages of decay.

The fungus can cause as much as 20 per cent loss in weight in small blocks of pine sapwood after about four months' exposure at 22° C. (8).

Sexuality as exhibited by cultures.—Lenzites saepiaria is a heterothallic species (21). Bipolar segregation has been noted by Fries (12). Results obtained by Mounce and Macrae (16) in Canada likewise show that complete interfertility exists between haploid mycelia derived from different sources. In one experiment Robak (21) reports that seventy-nine of eighty-four pairings he arranged exhibited clamp connections. The negatively resulting pairings occurred when one strain or the two combined had been kept in culture for a long time.

Robak (21) investigated Canadian and Norwegian strains and

found them mutually fertile. The interfertility was not absolute, however; the ages of the cultures were given as a possible explanation for this.

Reaction to chemicals.—Extracts from wood have been studied with reference to their toxicity to *Lenzites saepiaria.* Extracts of *Pinus ponderosa* were tested, for example, by Anderson (1). He did not find the extract from the heartwood to be much more toxic than that from the sapwood. Resistance to sodium fluoride was tested by Richards (20), who has arranged a number of wood-destroying fungi according to their reaction to this chemical, beginning with the most susceptible: *Poria incrassata, Polyporus abietinus, Pol. versicolor, Fomes roseus, F. pinicola, F. subrosea, L. saepiaria, Pol. hirsutus, F. Pini Abietis, F. annosus,* and *L. trabea.* The position of *L. saepiaria* is seventh in this list of eleven fungi.

Carswell and Nason (6), who studied the toxicity of other phenols to *Lenzites saepiaria,* report the amounts causing total inhibition of growth as well as death (Table I).

TABLE I

TOXICITY OF SUBSTITUTED PHENOLS TO LENZITES SAEPIARIA

The figures give the percentages of the chemical in the medium.

Causing total inhibition of growth				Causing death			
Penta-chloro-phenol	Sodium penta-chloro-phenate	*B* naph-thol	*p*-chloro-*m*-cresol	Penta-chloro-phenol	Sodium penta-chloro-phenate	*B* naph-thol	*p*-chloro-*m*-cresol
0.002	0.002	0.01	0.01	0.006	0.004	0.05	0.04

Decay: Gross features.—The first indications of rot caused by *Lenzites saepiaria* is a pale-yellow discoloration, accompanied by brittleness and softening, especially in the springwood. Later the wood becomes brown and breaks into cubes by cracking along and across the grain. Little or no superficial mycelium is visible. It has been pointed out by Cartwright and Findlay (9) that, when a cross section of an infected beam is viewed, isolated patches of dark reddish-brown areas may be seen and that, when the decay is more advanced, the cubical rot becomes evident owing to the formation of checks and the separa-

tion of the annual rings. As they state, "Decay is usually confined to the interior of a beam, which may become completely rotted away internally, but yet continue to have a more or less unaltered skin."

Microscopic features.—Only one or two hyphae are usually present in each tracheid, according to Falck (11). He therefore concluded that the hyphae may affect the cell walls for some distance. The hyphae in the wood exhibit many medallions. Yellow mycelium with thickened clamp connections is present in the tracheids beneath fruiting bodies.

Spaulding (27) observed few boreholes, and reported that the hyphae usually pass through the pits.

Decay in living trees.—If certain unusual environments are established that especially favor the development of fungi characteristically on wood products, they will attack living standing timber. *Lenzites saepiaria* was discovered in 1949 to be at least one cause for decay in standing green jack pine in the extensive and historical plantations on the Nebraska National Forest (Pl. IV). Similar injury has been observed in shelterbelt plantings in the area. The rot is the indirect result of pruning operations, but instead of occurring at the cutting wounds, it became evident initially at the extensive sunscald areas resulting as an aftermath of pruning (Pl. V).

It is apparent that the decay will finally lead to the total destruction of many of the jack-pine stands. The pruned pines exposed to the sun at the borders of the plantations show sunscald injury to approximately the height on the trunk at which the branches were removed. *Lenzites saepiaria* has been found to infect these trees, and the resulting rot weakens the pine, so that they break during storms (Pl. VI). The nearest adjoining rows then become damaged because of sunscald and rot (Fig. 1). Jack pines not pruned are not damaged, as were those trees with the branches removed (Pl. VII).

Plantings of *Pinus ponderosa* are protected from sunscald by their relatively thick bark (Pl. VIII). *Lenzites saepiaria* has not infected these trees through pruning wounds.

Enzymes.—Enzyme production for *Lenzites saepiaria* has been investigated by Zeller (28, 29). The following enzymes have been recorded: esterases, maltase, invertase, raffinase, emulsin, tannase, diastase, hemicullulase, cellulase, pectinase, inulinase, urease, hippuricase, nuclease, protease, erepsin, trypsin, rennet, catalase, tyrosinase.

FIG. 1. Sample occurrence of sunscald injury in pruned and thinned jack-pine plantation, Nebraska National Forest. The black parts of trunks define the relative extent of wounds (July, 1949). A dead tree is indicated in black. The rot appears at the sunscald instead of at the pruning wound. The weakened trees blow over, so that protected rows of pine are damaged in turn

and, to some extent, oxidase. Except for the last three enzymes, a greater amount of the enzymes was present in the vegetative tissue than in that of the fruiting body.

Resistance.—It is to be expected that the fungi which are resistant to high temperatures in agar cultures will be among the most resistant to them in wood. It will take longer to kill the fungi in wood, particularly if the wood is dry, than to kill those in agar cultures. Snell (24), using ¾-inch blocks artificially inoculated with *Lenzites trabea,* found that the fungus (together with others tested) was able to withstand 131° F. (55° C.) for twelve hours at moist heat, whereas it took 221° F. (105° C.) for twelve hours to kill all the fungi with dry heat.

Lenzites saepiaria in wood is one of the most resistant to heat. Montgomery (15) found that it was still alive after two hours at 60° C. in wood with an average moisture content of 63 per cent, but that it was killed after two and one-half hours' exposure to these conditions. These results correspond to those obtained by Chidester (10), who reports that the fungus was killed in moist heat maintained at a temperature of 150° F. (65.5° C.) for about one hour.

Prevention and Control.—Storage of pole, tie, and structural timbers must be off the ground and under conditions which provide ventilation. It is necessary to keep the yards free of debris and weeds which hinder air circulation. The time required to season poles (and other products) varies regionally.

Since *Lenzites saepiaria* is one of the common causes of rot in poles in place, several methods have been employed to treat such timbers; among them are the Cobra process and the Pfister methods. The soil is dug away from the poles and a paste preservative is injected at short intervals over an area above and below the ground line. The two processes are much alike, and differ chiefly in details of the construction and operation of the tools. Other processes provide for coatings of various types. Treated sections may be wrapped with building paper to prevent animals from being poisoned by the preservative.

Because it is difficult to obtain a continuous surface of charcoal around the pole and to prevent charcoal itself from breaking away, charring the poles at the surface of the ground is seldom practiced. Furthermore, *Lenzites saepiaria* can readily infect the charred pole through checks. Charring is sometimes used before standing poles are sprayed with a preservative.

Various types of treatment of poles, posts, and other timbers to prevent decay have been discussed elsewhere (3).

For thin-barked trees planted on sites subject to high temperatures, pruning should be avoided; at least on the rows of trees that are exposed to the sun at the margins of the plantation. Thinning practices should likewise be avoided at the borders of the forest. Jack pine grown on such sites is ordinarily best suited for fence-post timbers. The trees cut for posts may be limbed at the time of felling. In general, thick-barked trees such as ponderosa pine are not subject to sunscald. Juniper, although easily broken by winter storms, has not been damaged by sunscald in the plantings observed. Mixtures containing juniper may be used for such areas. Interplanting with either *Juniperus virginiana* or *J. scopulorum* in the more open stands subject to sunscald is urgently recommended.

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PLATES I–VIII

Intermediate forms of *Lenzites saepiaria* and *Trametes odorata* may be distinguished in culture more satisfactorily than by morphological features. This form even suggests *T. carbonaria*. Substratum white spruce, Moose Pass, Alaska

Lenzites saepiaria on white birch, Goose Bay, Labrador

Sunscald in jack pine plantation established in 1911. This stand was pruned and thinned. Nebraska National Forest. Photograph made in 1940

Fruiting body of *Lenzites saepiaria* at sunscald wound of pruned jack pine, Nebraska National Forest

Sunscald injury in jack pine at margin of plantation, Nebraska National Forest. Note the severity of the wounds, which extend to the approximate height of the pruning

Effects of *Lenzites saepiaria* in jack pine on trees at margin of plantation, Halsey, Nebraska. The fungus infected the trees, not at the pruning wounds, but at the sunscald injuries resulting from the operation. Destruction of the trees is inevitable

Pruned and thinned jack pine (left) and unpruned and unthinned stand (right). Sunscald injury appears in the pruned and thinned part of the stand

Ponderosa pine, pruned but not injured by sunscald because of the thick bark. No decay appears in these plantings

RECENT FOREST TAX LEGISLATION IN NEW HAMPSHIRE

J. WILLCOX BROWN

SITUATED between Maine and Vermont, New Hampshire comes naturally by its reputation as one of our more conservative states. In spite of the traditionally cautious approach of its people to any new tax measure, in 1949 the state legislature agreed to as comprehensive a substitution of the yield tax for the property tax on timber as has been attempted in any other state. In addition, a forest-conservation inducement was coupled with the yield-tax venture.

THE YIELD TAX IN THEORY AND PRACTICE

The theoretical imperfections of the yield tax as a revenue source alternative to the general property tax were highlighted in the report *Forest Taxation in the United States* (2), by Professor F. R. Fairchild and associates. On a nationwide scale, the primary importance of lightening the property-tax load through increasing the efficiency of local government was emphasized. Next, the investigators pointed out the importance of sounder administration and of more thorough collection of the property tax in the interest of all property owners. Finally, they admitted the unique handicap under which deferred-yield property labored, but declared that the yield tax was an inadequate solution because it imperiled the fiscal foundation of local government. While placing the position of deferred-yield properties in proper perspective as third in importance of the major deterrents to better forest practice, the taxation experts offered three alternative approaches to the yield tax as a solution. Of these proposed alternatives it is sufficient to say that none of them has received widespread support for enactment into law in any state. The yield tax, on the other hand, usually has been retained in those states where it existed in one form or another and repeatedly has been the basis for proposed legislation.

Opposition to the yield tax on practical as well as on theoretical grounds has caused modifications in it for the sake of expediency in those

places where it has been applied. For the most part yield-tax laws have been optional. Actually, very few timberland owners have classified their lands under the yield-tax provision in any state having the necessary optional legislation, such as Michigan or New Hampshire. In almost every case the yield-tax principle has been modified, so that a separate annual property tax is retained on the land, with the timber being subjected to a yield tax at the time of harvest. In several states the full property tax has been retained, but a severance tax at the time of harvest has been superimposed. In Oregon and Washington substitution of the combined land and yield tax for the property tax has been restricted to cutover lands. Before 1949 Mississippi was the only state in which the property tax on standing timber had been uniformly replaced by a yield tax. It imposes the yield tax at the nominal rate of 3 per cent.

THE SITUATION IN NEW HAMPSHIRE BEFORE PASSAGE OF THE NEW LAW

Against a background of nationwide caution in application of the yield-tax principle, New Hampshire's recent tax venture is not easy to understand. Forest land, covering about 84 per cent of the area of the state, is its major natural resource. Realization of the significance of the forest resource undoubtedly was a factor in the change, but a comparable situation in certain other states has not yet prompted similar action in them.

The local tax picture that existed in New Hampshire prior to the passage of the new law shows more clearly the reasons for action. The tax base is notoriously narrow, having strict limits imposed by meager natural resources. Other restrictions have been added either by the state constitution or by legislative reluctance to supplement the general property tax with newer types of taxes. The tax burden, on the other hand, is inevitably high because of a diverse settlement pattern in rough mountainous country, with correspondingly high costs for provision of public services.

This diverse settlement pattern is perpetuated through the structure of local government. The state has a land area of 9,302 square miles, amounting to a little less than 6 million acres. This area is divided into 234 organized towns and cities, with 22 additional "unincorporated places" in the more isolated mountainous localities. These 256 units are in turn grouped into ten counties. It is in the New England towns that

our purest form of democracy persists, being displayed annually at the March town meetings.

From various sources I have estimated that total revenues of about 25 million dollars were necessary to meet local governmental expenses in New Hampshire in 1945–46 (1). The general property tax was the major single source of local revenue, totaling roughly 19 million dollars. Thus slightly more than 75 per cent of the local tax burden was resting on the general property tax. Miscellaneous local sources accounted for an additional 18 per cent of the local revenues. The state-assessed taxes distributed to the towns, including the railroad tax, savings bank and building and loan tax, insurance tax, and the interest and dividends tax, provided slightly less than 4 per cent of the total local revenue. Essentially these are taxes on intangible property, collection of which has been shifted from the towns to the state. It is significant that less than 3 per cent of the total local revenues apparently was provided through other state and federal payments and grants. This situation is a far cry from Michigan's sales-tax diversion.

The total property tax per acre offers an additional means of comparing the property-tax burden in New Hampshire with the situation in Michigan. In the absence of any recent published statement of the amount of the property tax per acre on rural New Hampshire land, I have endeavored to compute a per acre tax on rural values from the State Tax Commission reports (1, 4). The result obtained has necessarily been an approximate one. The taxes for the eighteen towns and cities classed by the census as urban were completely excluded from the state totals. The tax attributable to land, timber, and buildings in the remaining towns and in the unincorporated places was considered to represent basically rural values. Dividing the total number of rural acres into the amount of tax derived as indicated gives the following rural tax per acre for representative years: $.38 in 1913; $1.13 in 1929; $1.13 in 1938; $1.25 in 1946. The figures are not equivalent to the tax on farm real estate since they inevitably include the tax on land and buildings in villages.

The situation in Michigan furnishes an interesting contrast. Farm real-estate taxes per acre here were $.54 in 1915; $1.38 in 1929; but only $.44 in 1938. A special study by one of Professor Fairchild's associates (3) showed that the reasons for this decline in tax per acre during the depression years were: (*a*) the lowering of assessed values, (*b*) a constitutional amendment limiting the tax rate to a maximum of 15 mills, (*c*)

the adoption of the retail sales tax by the state, and (*d*) increased state financial aid to local governments. Local governmental costs did not decline, but other measures reduced the pressure on the property tax and virtually eliminated the demand for special forest-tax legislation in Michigan.

The state government in New Hampshire also has a narrow tax base. Its chief source of undesignated revenue is the taxation of minor "vices." A canny form of Puritanism has led to the taxation of racing, tobacco, and beer, and a mark-up on liquor sold at state stores. The purpose is to secure a maximum income which depends upon preservation of the goose that lays these golden eggs. Certain state functions such as highway construction and fish and game propagation are financed through earmarked revenues. A major reason why the state aid to local government is so skimpy is that the undesignated revenues are insufficient to permit sizable grants. The proponents of various measures for broadening the revenue sources of the state have not succeeded in uniting to push through a program. Proposals for a sales tax or a net-income tax were again killed in the 1949 legislature. A new proposal for a gross-income tax was also defeated. Rural representatives have played a prominent rôle in rejecting new taxes.

The political situation is difficult to analyze. Though the rural proportion of the total population declined from 83 per cent in 1850 to 42 per cent in 1940, the rural areas have maintained a strong position in the state legislature, with its house of 400 representatives. So tightly have the towns clung to their prerogatives that they have come to be known as the "little republics." At present it is stipulated that every town, regardless of size, shall be represented in the legislature in at least one session out of five. At the last constitutional convention a referendum providing for representation of every town at every session was drafted for submission to the voters. It almost secured the necessary support at the general election to become a constitutional amendment.

Most of the representatives of the small towns and the rural areas are Republican, but the industrial centers elect many Democratic representatives. The opposition to and the support for forest-tax reform, however, have been essentially nonpartisan. A sustained drive for a change in forest taxation dates back more than forty years. Pressure for the change has been maintained because of failure of the state to secure any adequate alternative source of revenue to lighten the property-tax load.

Spearheaded by the Society for Protection of New Hampshire Forests, the drive for forest-tax reform has had the official support of almost every organization in the state. In 1942 the state constitution was amended to encourage special tax treatment of growing wood and timber. The following year the legislature took the first step in this direction by requiring the separate assessment of growing wood and timber, though this class of property was still to be taxed at the same rate and on the same basis as other property.

Finally, in 1949 the alert regime of Republican Governor Sherman Adams gave the impetus to secure passage of the yield-tax measure. In supporting the new law the Governor brought to bear his first-hand understanding of the forest-tax problem gained as the woods boss of one of the larger pulp and paper companies operating in the state. It appears strange that the strongest opposition came from the small towns, which form the backbone of the state's Republican organization. Yet there was more logic in the rural desire to prevent reduction of the property-tax base than in the rural refusal to extend taxation to predominantly urban classes of revenue.

FEATURES OF THE NEW TAX LAW

The act relating to forest conservation and taxation which became Chapter 295 of New Hampshire Laws of 1949 is an adroit combination of answers to many previous objections to the yield tax. First, it releases nearly all classes of growing wood and timber from the general property tax and substitutes a yield tax of 10 per cent of stumpage value, to be assessed at the time of cutting. Second, the property tax on forest land is retained. Third, the yield tax is to be administered locally. The selectmen, who are the local assessing officials, will levy the tax, and the income from it will be expended for local purposes, for local control has a strong appeal in New Hampshire. Fourth, the law has been so designed that it will apply to cutting operations on the White Mountain National Forest. This has increased its popularity with north-country residents.

Much opposition to forest-tax reform has been based on the fear that the amount of local revenues either would become unpredictable or would be seriously reduced. The law takes care of this by providing for reimbursement by the state for each town to the full extent of any loss in tax revenue not covered by the new yield tax. The creation of a special state fund is authorized as a source of such reimbursements. The sum of $300,000 can be set aside from the treasury or can be raised by issuing

bonds. The bonds, if issued, are to be retired through the annual earmarking of not more than $25,000 from the Forest Improvement and Recreational Fund, which consists of revenues accumulated from the operation of state parks and forests.

A unique feature of the new law is an attempt to encourage forest conservation through the abatement of 30 per cent of the yield tax for cutting in accord with approved standards. The owner who qualifies for this abatement will have his stumpage taxed at the rate of 7 instead of 10 per cent of its value. Minimum cutting standards are being recommended to the state forester by the District Forest Advisory Boards. These standards are to become effective upon approval by the state forester with the advice and consent of the Forestry and Recreation Commission. It appears that the restrictions placed upon the operator through these standards will be rather nominal, at least initially.

ADVANTAGES AND DRAWBACKS OF THE NEW LAW

It has always seemed paradoxical to those unfamiliar with the workings of the New Hampshire property tax that such concern over its heaviness should go hand in hand with an amazingly small amount of tax delinquency. Passage of the law has brought into the open the extent to which the property tax on timber had been guided by the principle of ability to pay rather than by the full value. This situation has been revealed through the charge that the new tax favors the owner of large holdings, frequently a nonresident, at the expense of the resident with smaller holdings. Selectmen do not hesitate to admit now that they have had a searching eye for timber values on properties acquired by summer residents and by lumber and pulp companies. As a result, lifting of the old tax is proving beneficial to the nonresident owners while offering no relief to the resident whose timber values went relatively unnoticed. It is thought by some advocates of the new law that this may force the reconsidering of the whole question of property-tax administration. In any event it seems advantageous to have a clearer picture of the subjective interpretations of the property tax which often have prevailed in the past.

Some rural residents, however, claim the law is a screen for subsidy in the form of tax concessions to large operators under the guise of promoting forest conservation. This attitude was expressed by a number of resident owner-operators of small holdings after the passage of the law in the summer of 1949. Some stated that they intended to strip off their

timber before the new law went into effect in the spring of 1950. Fortunately for the condition of the woods, the market in the winter of 1949–50 was unable to absorb an excessive supply. Large operators generally are pleased with the law, and some are planning to expand and improve their holdings. The quieting of the antagonism of rural residents may well depend on the good faith of larger owner-operators in applying high standards of forestry to their own lands.

If it is true that much forest property in the state has been underassessed, then the great need for forest-tax reform is not immediately evident. Aside from the unequal application of the property tax, however, the threat of sudden arbitrary increase in valuation serves as justification for the change. Once the new law is in effect, owners will have no pretext for stripping their timber to lighten their tax burden. On the contrary, the new law offers an incentive for harvesting only the higher-value timber and for building up the growing stock through preserving the lower-value young trees from premature liquidation.

A possible disadvantage of the yield tax is that owners of mature timber with recreational value will hold it off the market indefinitely if they are immune from taxation. This drawback is taken care of by a clause in the New Hampshire law stipulating that, upon attaining maturity, any timber stand may be declared by the assessing officials as again eligible for imposition of the property tax. The catch lies in obtaining a sound and generally acceptable basis for determining maturity.

Theoretically, the combined land and yield tax also has the drawback of penalizing the poorer sites if a uniform land tax is applied. This objection can be met in New Hampshire through adjustment of the land tax to the productivity of the site at the discretion of the assessing officials. Again the problem lies in finding an adequate basis for determining productivity.

A major advantage of the new law that received little publicity during the campaign for its passage is the spotlight that will be focused on the customary lump-sum timber purchases. The operator who contracts to buy timber becomes the owner in the eyes of the law. In the return that he is required to file with the assessing officials he must state the kinds and amount of timber cut. This divulging of trade secrets of the lump-sum buyers may cause reform of their practices or force them out of business. Operation on a scale purchase basis is considered more conducive to good forest practice.

Another disadvantage of the law that may prove its greatest practical

obstacle is its passage in advance of any alleviation of the overall tax situation. The $300,000 authorized for the reimbursement fund is the sum estimated as necessary to meet the deficits of the individual towns during the first year of operation of the new law. The advocates of the yield tax have some grounds for hope that it will produce a larger revenue than originally anticipated. This hope is based on the substantial areas of underassessed timber that may come onto the market fairly continuously. If their expectations do not materialize, it may prove politically impossible to secure repeated appropriations of $300,000 a year to keep the reimbursement fund solvent. The total of $3,000,000 over a ten-year period is an item not to be lightly dismissed in a state which had to institute a rigorous austerity program at its last legislative session to balance its budget.

In summary, most of the obstacles to the law lie in the substitution of a new set of administrative problems for the old ones, which had become case-hardened by a long tradition of expediency. If the lack of expedient local by-passes for the new problems causes greater reliance on the guidance of the state's forestry agencies and of the State Tax Commission, the change may be a wholesome one. The major threat to the new law may prove to be the lack of adequate state financial strength to bridge the gap in yield-tax revenue while the forest resource is being built up to a higher level of sustained production. Here, too, the setting of the whole tax situation in a new perspective may foster reconsideration of their own best interests by small-town residents who have been the mainstay of New Hampshire democracy. It is a heartening step that, since passage of the law, Governor Adams has assigned two well-qualified men to serve as emissaries to the hinterland. Rural support for the law is increasing with an understanding of the contribution that its proper application can make to the rural economy.

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THE MONTANA CONSERVATION COUNCIL

A SIGNIFICANT EXPERIMENT IN CONSERVATION ORGANIZATION

KENNETH P. DAVIS

TO EVALUATE the significance of the Montana Conservation Council it is necessary to have some general understanding of the situation in which it developed. Here are a few key points.

Montana lives almost entirely on its natural resources; it is a producer of raw materials. A half million people thinly occupy its 94 million acres as compared to 6 million people on 36 million acres in Michigan. While the per capita wealth of the state is high, it is low in view of the demands its physical size places on furnishing the services we have come to expect in these United States in terms of roads, educational facilities, and the like.

The state includes very large wild-land areas, most of which are in public ownership, largely Federal. This is particularly true of forest lands, since nearly 80 per cent of the total forest area of 24 million acres is in the national forests. The activities and services of the Federal agencies in conservation are correspondingly large. Most of the technicians in the state are federally employed.

The volume and coverage of natural-resource services the state supplies are small compared to its large interest in these resources, especially as regards wild land. This is particularly true of wild lands. It has nothing approaching the Michigan Department of Conservation in conception, organization, scope, or financing. In forestry the state has a state forester and good supporting legislation. However, his office is seriously underfinanced, and his work is limited almost entirely to fire control and timber-sale administration on state-owned forests. There is a strong School of Forestry at Montana State University, which over the years has exerted large leadership and influence in forestry and wild-land conservation matters, although its actual facilities are largely limited to teaching. In agriculture the state coöperates with the Federal Government in supporting an excellent research and extension organization through the land-

grant college system. In wildlife there is an active and developing Fish and Game Department. Collectively, however, state conservation agencies are weak and particularly so as compared with those of the Federal Government.

Nevertheless, there is a large, deep, but somewhat inarticulate popular concern over the wise use of Montana's natural resources that is emerging through the atmosphere of exploitation which has dominated its history and outlook in the past. After all, the state is scarcely more than a generation removed from the actual frontier, where natural resources were something to conquer and tame. I am convinced that the people of the state have developed tremendously in their conservation awareness and thinking in recent years, but this thinking is more or less latent.

It was in this general situation that the Montana Conservation Council developed. Its immediate beginning was in August, 1948, when people representing seventeen different organizations and groups met at the state university in Missoula for a general conservation conference. The Council emerged from this conference. Its basic purpose was to serve as a common meeting ground, a popular front, through which all groups interested in conservation could be effective in furthering a more general understanding and application of conservation. The specific objective was to promote conservation education in Montana on the broadest possible basis. This was recognized by everyone as a prime need requiring concerted action for effective progress.

The Council was kept informal, with no written constitution and by-laws—nothing more formal than the motto adopted, "Conservation is everybody's business," which well expresses its general philosophy. Anyone may become a member by the simple act of participation. It happened that I was named president of the organization, being at that time in Montana, my native state, serving as dean of the School of Forestry at Montana State University.

At that meeting in August, 1948, the newly formed Council undertook two major projects. The first was an adult education project, specifically organization of a conservation caravan to make a field-study tour of Montana resources and their use. The general idea was that seeing is understanding; that only by getting key people representing various organizations and groups together on the ground for a trip of some duration could the many-sided nature and interrelations of natural-resource use be comprehended. The second job was to promote and strengthen conservation education in Montana schools.

The conservation caravan turned out to be a highly successful venture. Decision to hold a caravan tour in the summer of 1949 was made and a working committee organized. The inevitable meetings were held, and plans took form. A six-day trip in western Montana was planned in detail with an itinerary insuring a well-rounded picture of the use of natural resources in forestry, agriculture, wildlife, and recreation. Tour information was sent to many individuals and organizations, and as much publicity generated as possible. Then came the questions. Would people and organizations accept this new Council in an already complexly organized field as meaning business and offering something? Would they sponsor the sending of representatives and pay their way since the caravan and Council had no financial resources and the trip had to be self-supporting? The aim was that after the tour each individual would return to his own group able to give a broader picture of what conservation is and means on the ground. Yet organizations are understandably slow to finance sending their members on an untried venture and particularly one that might seem like a mere junket. The whole idea was new; there were no precedents.

But the idea had vitality and received support. The Montana Association of Soil Conservation District Supervisors supported the caravan and appointed representatives. The Western Montana Fish and Game Association, a forward-looking group, voted to send a high-school and an elementary-school teacher from Missoula on the tour. Winton Weydemeyer, Master of the state Grange and a deeply thinking conservationist, gave it active support and enlisted participation by the Grange people. The Montana Federation of Labor was keenly interested and sent three representatives. The various Federal and state conservation agencies gave active help, as did the University and the State College. And so the idea slowly became a reality.

By the take-off day of July 18, 1949, an extremely well-balanced group was ready to go. It included three ranchers representing the Grange and Soil Conservation District Supervisors, three lumber and sawmill workers representing the labor organizations, two housewives, a high-school student, a high-school principal, a high-school teacher, two elementary-school teachers, a businessman-sportsman representing a chamber of commerce, a lumber salesman representing the Anaconda Copper Mining Company, one member each from the Federal Forest Service, Soil Conservation Service, and Bureau of Land Management, the state extension forester, a professor of forestry, and a professor of

geography representing the University and the State College, respectively.

This was the diverse group of twenty-one people, many of them unacquainted, who faced each other in a chartered bus one Monday morning. Most of them probably secretly wondered how such a group would get along for a full week of travel. As the tour leader I, too, certainly wondered.

It worked out amazingly well, better than any of us imagined it could. The group quickly became welded together through the ready acquaintanceship of travel. Though all were concerned with conservation, individual interests were often limited in scope. This trip assembled the picture as a whole. It showed the basic interdependence and unity of mountains and valleys, of streams and crops, of timber and industry, of agriculture and wildlife. It demonstrated the common interest in conservation of dissimilar occupational groups, between housewives and sawmill workers, foresters and soil conservationists, college professors and ranchers, high-school teachers and sportsmen, trade unionists and businessmen.

The tour began with an outstanding day in the famous Bitterroot Valley in southwestern Montana. The varied natural resource situations and problems of the valley were presented mostly by landowners themselves, thirteen people taking part. The itinerary was arranged by A. J. Patterson, a Hamilton rancher, who did a remarkable job of both planning and execution. The day in the Bitterroot was followed by five more equally educational days in western Montana. While the scene changed greatly from day to day with the varied nature of the territory, the basic theme and pattern were the same. For many people, the state and its situation were viewed in a new light. A common remark was: "I've been through this country before but have never really seen it until now."

The success of the trip was largely due to two things. The first was the large number of people participating. In addition to the caravan members themselves, sixty-one local people took an active part in discussions and descriptions. Many more met the caravan from day to day and a number of them traveled with it for a day or two. The second was the fine group spirit and understanding that developed. Traveling together in a bus had much to do with this; it probably could have been achieved in no other way. A loud-speaker system made it possible to talk effectively en route and avoided many time-consuming and tiring stops. The caravaners were royally fed and entertained with the best of Montana hospitality.

The plan is to continue these tours as recurrent affairs, covering a different portion of the state each year. With an area of approximately 147,000 square miles there is ample space for three or four entirely separate tours. Two may be conducted simultaneously if the demand justifies. So much for the caravan as an experiment in adult and organization education in conservation.

Another closely related enterprise beginning independently, but later becoming more or less allied with the Council, was a series of radio programs on natural resources and their conservation given during the winter of 1948–49 in western Montana. There are a number of agencies and groups in and around Missoula interested in conservation in one way or another. It was proposed that they work together on a series of radio programs. A local radio station, KGVO, agreed to sponsor three fifteen-minute programs a week as a local-service feature, but could offer little assistance in script preparation. Over a thirty-week period ninety programs were put on by something more than twenty agencies and groups. It might be of interest to mention a few to give an idea of the range of interests involved: the Western Montana Fish and Game Association, Montana Federation of Garden Clubs, the Forest Service (both the research and the administrative branches), the Soil Conservation Service, the Farmers' Home Administration, the University (both forestry and biological science groups), the Farmers' Union, State Forester, State Fish and Game Department, Lumber and Sawmill Workers' Union, and the Missoula Chamber of Commerce.

The general theme, stated by the radio announcer at the beginning of each broadcast, was "Conservation of Your Natural Resources, the Lifeblood of Montana." Within this theme each agency or group was free to develop a program or programs built around its own interests and work.

It could not be said that all the programs were polished presentations. Scheduling ninety programs on a minimum of organization and strictly among amateurs was a difficult matter. Having served as chairman of the scheduling committee I know. I can well recall times when the radio station asked where was the next program, the call coming an hour or two before it was scheduled to go on the air. However, the programs were original, local in origin, and some of them very good. Collectively, they gave a good account of the use and conservation of resources, and their public reception was favorable. Of importance probably equal to the public benefit was the fostering of mutual acquaintanceships and better understanding among the various groups and agencies participating.

As earlier stated, the second major project of the Council was to strengthen conservation education in Montana schools. In furtherance of this a conference was called by the Council at Montana State University in the summer of 1949. The meeting was organized by the Conservation Education Committee of the Council under the chairmanship of Dr. Harold Tascher of the University. It was an excellent meeting well attended by representatives of most of the educational institutions and organizations of the state. The whole problem of conservation education in the schools and its recognition as a part of teacher training was thoroughly discussed. Constructive recommendations were made and presented to the State Board of Education and to all other agencies and organizations concerned. One concrete outcome was the holding of a conservation workshop as a part of the University's summer session of 1950. This marks a definite move to strengthen teacher training. Another specific outcome of the meeting is preparation of a bulletin on Montana's resources and their use for the schools.

Another project under the general auspices of the Education Committee, but resting primarily on the initiative and energy of a member of the Council for its execution, is initiation of a series of conservation "show-me" trips and talks at biweekly intervals for those in the sixth and higher grades in the Washington School at Anaconda. Mrs. Carolyn Madden of Anaconda, secretary of the Council, is leading this enterprise and reports enthusiastic response by students, teachers, and parents. It is an experiment in community-conservation education with large possibilities.

As shown by these various activities, the Conservation Council is on its way to becoming a force in Montana. It is an interesting adventure in relationships. The Council works primarily through its members, whether individuals or groups. Being composed of diverse elements, it can act as a unit only on matters of general import and agreement.

Its primary value is probably in bringing people and organizations together. I have seen many instances of this during the period I worked with the Council. One of them concerns the University and the State College, the relationship of which is analogous to that between the University of Michigan and Michigan State College, although in Montana all the institutions of higher learning are under the general administration of a chancellor. This does not, however, keep the University and the College from eyeing each other. From the start care was taken to avoid identifying the Council as the offspring of any particular institution, though it has been consistently maintained that overall leadership of the

Council should come from the educational institutions of Montana. Such matters put much premium on good faith and mutual trust. As concrete evidence of good relations, leadership of the Council was shifted in 1950 from the University to the State College. It is believed that the Council has been a force in strengthening rapport between these two institutions, and the same can be said as regards other agencies and groups brought together through the Council.

All in all, a fine start has been made in Montana, significant in development of that feeling of unity and wide understanding with which conservation must be approached. It is indeed everybody's business.

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RED PINE GROWTH TEN YEARS AFTER THINNING

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INTRODUCTION

RED PINE was once an important component of the famous pine stands of the Lower Peninsula of Michigan. Repeated fires after logging largely eliminated any young growth that might have partially replaced the virgin pine, so that today there is only a very small area of natural red pine. This species, however, has been a favorite one for planting. Of the half-million acres of forest plantations in Lower Michigan, probably 45 per cent are in red pine. These plantations are still in the early stages of development, and few have reached merchantability—even for small-sized material such as pulpwood.

Red pine is rated as an intolerant tree (1), but one that tends to stagnate in dense stands (4). Good response to thinning has been reported in Minnesota (5) and in Wisconsin (6). Published information on thinning of red pine on the sandy soils of Lower Michigan has been completely lacking. Consequently, any information on red pine growth and development in response to thinning in the northern part of the Lower Peninsula should be of interest.

STAND DESCRIPTIONS

Two red pine stands were selected for study by the Michigan Conservation Department in 1934. One was a densely stocked plantation representative of the earlier reforestation efforts, and the other an overstocked natural stand.

The red pine plantation is located on the Higgins Lake State Forest in Crawford County. It was established in the fall of 1912 with 3–0

stock. Trees were planted in horse-plowed furrows with a spacing of 5 × 5 feet. This spacing resulted in a stand of 1,740 trees per acre. The planting area was an open field that had once been cultivated for crops. The survival of trees to 1934 was 85 per cent. The site, a level area of Grayling sand, is classed as poor to medium in productivity (site index 46 at 50 years), according to site-index curves for red pine (2).

The natural stand of red pine, located on the Houghton Lake State Forest in Roscommon County, is dense and even-aged, with some scattered white pine, jack pine, and oak. From increment borings the stand was estimated to be 38 years of age in 1934. Basal scars indicate that surface fires have passed through the stand, but it is likely that this particular area escaped being heavily burned after logging. A few scattered red pines from the original stand are still present. Specific factors contributing to the establishment of this exceedingly dense stand are not known. The soil is Rubicon sand on a level and low situation. This site is also classed as poor to medium for red pine (site index 46 at 50 years).

The sites for both the plantation and the natural stand appear to be quite similar. The plantation is on a soil series (Grayling) that might be classed as poorer in productivity than Rubicon, but soil type alone is not the whole answer in evaluating sites. The cultivation of the plantation area previous to establishment improved the site at least temporarily, whereas the heavy stocking may have reduced the apparent site index of the natural stand.

THE THINNINGS

In 1934 both stands were thinned very lightly. These thinnings were so light that in 1939, five years later, the effects were hardly noticeable. About all that was accomplished was the removal of suppressed trees. In 1939 it was decided, therefore, to thin more heavily. The plantation at that time was 27 years old (30 years from seed) and was reduced to 620 well-spaced, good-quality trees per acre. The 43-year-old overstocked natural stand was thinned more lightly, since it was feared that snow breakage and windfall would result if the stand of spindly trees was opened up very much. Here 1,100 trees per acre were left. Stand conditions after thinning are summarized in Table I.

To follow the growth and development of the thinned and unthinned portions of these two red pine stands half-acre permanent plots were laid out in the thinned stands and $\frac{1}{4}$-acre plots in the unthinned stands. Individual tree measurements consisted of d.b.h. to the nearest one-tenth inch,

total height, crown length, crown width, and crown class. In 1949, ten years later, the trees were remeasured for growth, changes in stand structure, and mortality.

TABLE I

STOCKING PER ACRE OF THINNED AND UNTHINNED STANDS IN 1939

Item	Plantation		Natural stand	
	Thinned	Unthinned	Thinned	Unthinned
Trees, number.....	620.0	1,524.0	1,100.0	3,668.0
Basal area, square feet	65.0	131.3	102.2	167.9
Volume, cubic feet....	690.4	1,274.4	1,492.3	2,150.8

RESULTS

Diameter Growth

Diameter growth was increased considerably by thinning in both stands. The dominant and codominant trees on the thinned plots grew almost twice as much in diameter as corresponding trees on the unthinned portion of each stand (Table II).

TABLE II

DIAMETER GROWTH IN INCHES OF THINNED AND UNTHINNED RED PINE BY CROWN CLASSES, 1939–49

Crown class	Plantation		Natural stand	
	Thinned	Unthinned	Thinned	Unthinned
Dominant.....	2.52	1.28	1.86	1.32
Codominant.....	2.02	.78	1.23	0.68
Intermediate.....	1.65	.38	.57	.21
Overtopped.....	....	....	.24	.04

Crown dominance alone in a stand does not necessarily insure good growth, because dominance is a relative term for a particular stand. This is revealed in Table II, which shows that growth of dominant trees in different stands ranged from 1.28 to 2.52 inches at d.b.h. The best growth

was attained in the thinned plantation, where the dominant trees had very little side competition and had green crowns covering almost 60 per cent of their total height. Since the natural stand was not so heavily thinned as the plantation, growth was somewhat less. If thinned more heavily, the trees in the natural stand probably would have grown as well as those in the plantation. On the basis of results of these thinnings, it appears that an average diameter growth of two inches in ten years on crop trees can reasonably be expected in similar stands when under management.

Height Growth

Height growth was found to be closely correlated with crown class, being best on the dominants and the codominants (Table III). Of more importance, however, was the significant response in height growth made in the thinned natural stand. In contrast, height growth in the thinned part of the plantation was not significantly better than that on the check plot. Apparently the competition in the unthinned part of the plantation had not yet become severe enough to reduce height growth, whereas the severe competition in the unthinned natural stand has definitely retarded height growth.

TABLE III

HEIGHT GROWTH, IN FEET, OF THINNED AND UNTHINNED RED PINE BY CROWN CLASSES, 1939–49

Crown class	Plantation		Natural stand	
	Thinned	Unthinned	Thinned	Unthinned
Dominant and codominant	11.6	10.9	11.0	8.9
Intermediate	...	9.9	8.7	5.4

The results indicate that it is not necessary and, in fact, not desirable to maintain a dense stand for the best height growth. On the other hand, height growth might be retarded if the stocking is reduced too severely. However, the point at which this occurs is not known.

Volume and Basal-Area Growth

Before 1939, when the plantation was twenty-seven years old, there was very little mortality due to stand competition. Thereafter the rate

of diameter growth on the untreated plot decreased and mortality increased. Thus, for its effect on growth, the thinning was made at the proper stage in the development of this plantation, which was originally planted 5 × 5 feet. In spite of the reduction in basal area by one half and in the number of trees by over one half by thinning, the total volume growth continued to be as good as that on the unthinned plot, and the basal area growth was higher (Table IV). The average diameter of the main stand was about four inches in 1939, so that the high cordwood growth was due primarily to ingrowth of trees to merchantable size of five inches. The thinned plot now has as much cordwood volume as the unthinned plot, and it is on much larger trees, an important feature from the economic viewpoint.

The natural stand was already fully stocked in 1934, and mortality has been severe since then. In 1939 the stand, at age 43, had almost stagnated. The thinning removed over two thirds of the number of trees and over one third of the basal area, but after the thinning there was still some mortality. Basal-area growth after thinning was almost double that on the unthinned plot, but volume growth was about the same (Table IV).

TABLE IV

BASAL AREA AND VOLUME GROWTH PER ACRE, 1939–49

Item	Plantation		Natural stand	
	Thinned	Unthinned	Thinned	Unthinned
Basal area, square feet	77.5	59.5	47.7	25.2
Volume, cubic feet....	1,381.0	1,332.0	1,159.3	1,391.2
Volume, cords *.....	18.90	15.36	13.04	13.35

* Rough cords to 4-inch top d.i.b.

From a comparison of all plots in Table IV it appears that similar young red pine stands on low to medium sites of this type are capable of producing about 130 cubic feet of wood per acre per year.

Stem Taper

Stem taper varied with stand density. The trees on the thinned plots in both stands had greater taper in 1949 than those on the unthinned plots. The trees in the natural stand had much less stem taper than those

in the plantation (Table V). This reduced taper evidently resulted from the continuous dense stocking in the natural stand.

TABLE V

RELATION OF D.B.H. IN INCHES TO TOTAL HEIGHT IN 1949

Total height in feet	Plantation		Natural stand	
	Thinned	Unthinned	Thinned	Unthinned
30	4.5	3.5	3.1	2.5
35	5.8	5.0	3.8	3.1
40	8.0	7.6	4.7	3.9

Additional evidence of the effect of thinning on stem taper can be found by analyzing diameter and height growth for the period. In both stands diameter growth per foot of height growth was highest in the thinned stands. In other words, the trees in the thinned stands were becoming stockier than those in the untreated stands. Likewise, when dominant trees are compared with intermediate trees within any stand, the dominants are found to have grown more in diameter per foot of height growth. Dominant trees were becoming stockier than intermediates.

Spacing

Spacing between trees ranged from 3.5 feet in the unthinned natural stand to 8.4 feet in the thinned plantation. Stand density given in terms of spacing alone cannot be compared between the two stands because of the differences in age and tree sizes. Spacing given as a percentage of total height of the trees (7) accounts, however, for both site and age, so that all the plots may be compared in this respect. Table VI gives a comparison of the spacing-height ratio on the different plots. The natural unthinned stand has been in a state of equilibrium in terms of the spacing figure. This figure may actually increase as the stand becomes older and thins itself. All the stands had almost the same cubic-volume growth, but the stands with higher spacing values had better diameter growth, height growth, and basal-area growth. The best overall growth was in the

thinned plantation, where the spacing value ranged from 29 per cent after thinning in 1939 to 21 per cent in 1949. The results agree with the recommendations of Eyre and Zehngraff (3) for desirable spacing-height ratio.

TABLE VI

SPACING AS A PERCENTAGE OF TOTAL TREE HEIGHT

Year	Plantation		Natural stand	
	Thinned	Unthinned	Thinned	Unthinned
1939	29	20	19	9
1949	21	15	15	9

Changes in Stand Structure

Differences in the distribution of trees by diameter classes are already evident in the plantation ten years after thinning (Table VII). In the natural stand the only evident change due to thinning is the reduction in the number of trees in the smaller diameter classes (Table VII).

TABLE VII

NUMBER OF TREES BY DIAMETER CLASSES IN 1949

D.B.H. in inches	Plantation		Natural stand	
	Thinned	Unthinned	Thinned	Unthinned
0–4	48	632	628	1,840
5–6	304	736	238	348
7–8	250	92	122	112
9–10	18	0	34	40
Over 10	0	0	26	8
Total	620	1,460	1,048	2,348

Thinning changed the distribution of trees by crown classes considerably in the plantation but to a lesser extent in the natural stand (Table VIII).

TABLE VIII

PERCENTAGE DISTRIBUTION OF TREES BY CROWN CLASSES IN 1949

Crown class	Plantation		Natural stand	
	Thinned	Unthinned	Thinned	Unthinned
Dominant and codominant	88	68	29	28
Intermediate	11	22	27	22
Suppressed	1	10	44	50

SUMMARY

Ten-year growth measurements on plots established in northern Michigan in 1939 in a 27-year-old red pine plantation and a 43-year-old dense natural stand were taken in 1949. The following comparisons and deductions can be made from an analysis of the data:

1. Diameter growth in both stands was definitely improved by thinning. In the plantation, growth of dominant trees was nearly doubled in the thinned area. In the more lightly thinned natural stand, growth of dominant trees was increased by about 40 per cent. It appears that diameter growth of two inches in ten years on crop trees is reasonable for these stands when under management.

2. Height growth improved as a result of the thinning. In the plantation, however, the difference between height growth in the thinned and the unthinned portions of the stand was too small to be significant. In the natural stand, height growth in the thinned portion was significantly greater than that in the dense unthinned area.

3. Total volume growth per acre was about the same on all plots, both thinned and unthinned, being about 130 cubic feet per acre per year. In the thinned stands, however, this volume is being put on fewer and larger trees, which will be merchantable sooner than those in the unthinned stands. In the unthinned stand much of the growth will be lost in mortality before the trees reach merchantable size.

4. Spacing when given as a percentage of tree height appears to provide a good indication of the degree of stocking in a stand. From the data it seems that a red pine stand needs thinning when spacing of the trees is less than 20 per cent of total height.

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